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NEW SPECIES AND RECORDS OF BIRDS (AVES: MEGAPODIIDAE, COLUMBIDAE) FROM AN ARCHEOLOGICAL SITE ON LIFUKA, TONGA

David W. Steadman

Abstract.—A new species of megapode, *Megapodius alimentum,* is described from bones excavated at the Tongoleleka archeological site, Lifuka, Ha`apai Group, Tonga. Two coracoids from the same site are referred to *Megapodius* cf. *molistructor* and *Caloenas* cf. *canacorum,* both extinct species otherwise known from late Holocene fossils on New Caledonia. Another coracoid from Tongoleleka is referred to *Ducula* cf. *david,* an extinct species recently described from an archeological site on Wallis (Uvea) Island. A single tibiotarsus, too fragmentary to be named, represents an extinct, undescribed species of *Ducula* that is larger than any congener, living or extinct. The first four extinct species from Lifuka are more closely related to Melanesian species than to those of eastern Polynesia. The occurrence of five extinct species at the Tongoleleka site indicates that late Holocene losses of land birds in western Polynesia may have been as severe as those in eastern Polynesia.

In 1984, Tom Dye of Yale University excavated a rich archeological deposit on Lifuka, Ha`apai Group, Tonga, known as the Tongoleleka Site. Situated in an ancient sand dune, the site consists of three strata (Layers II, III, and IV) that bear pottery. The lowest and oldest stratum is stratigraphic Layer IV, which mainly represents Cultural Unit III. Layer IV, buried by 1 to 1.5 m of more recent sand, yielded decorated Lapita pottery, believed on the basis of sites excavated elsewhere to date at 3500 to 3000 years B.P. (T. Dye, pers. comm.). Two radiocarbon dates on charcoal from the upper portion of the overlying stratigraphic Layer III are 2260 ± 60 years B.P. (Beta-14171) and 1370 ± 70 years B.P. (Beta-11243).

Among the 20 identifiable bird bones from Tongoleleka are 11 bones of land birds, all but two of which are from stratigraphic Layer IV. Six of these bones are from two species of extinct megapodes, four others are from three extinct and one extant species of columbids, and one is from the extant starling *Aplonis tabuensis.* Also recovered were shellfish and bones of fish, reptiles, mammals, and marine birds. All of the bones probably represent food remains of early Tongans.

The purpose of this paper is to describe the morphology and systematics of the extinct species of birds from Tongoleleka. Additional details of the chronological, stratigraphic, zoogeographic, and cultural contexts of these extinct species will be presented in a future publication.

Materials and methods.—The fossil specimens are cataloged in the vertebrate zoology collections of the Bernice P. Bishop Museum (BPBM). Modern skeletal specimens are from the Division of Birds, National Museum of Natural History, Smithsonian Institution (USNM). Fossils from New Caledonia are from the Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris (MNHN). Osteological terminology mainly follows that of Baumel et

Fig. 1. The tibiotarsus of *Megapodius* in cranial (A–C), medial (D–F), and lateral (G–I) aspects. A, D, G, Holotype of *Megapodius alimentum*, new species, Lifuka, Tonga, BPBM 165686; B, E, H, *M. freycinet freycinet*, male, Halmahera, Northern Moluccas, USNM 557015; C, F, I, *M. pritchardi*, sex unknown, Niuafo'ou, Tonga, USNM 319633. Scale bars = 10 mm.

al. (1979). Measurements were taken with dial calipers with increments of 0.05 mm, rounded to the nearest 0.1 mm. CU = Cultural Unit.

Systematic Paleontology

Class Aves
Order Galliformes
Family Megapodiidae

Six specimens are referred to the Megapodiidae rather than to *Gallus gallus* of the Phasianidae, the only other galliform in Oceania, because of the following characters: coracoid–ventro-medial margin of humeral end of shaft more rounded, cotyla scapularis not extending beyond lateral margin of shaft in dorsal aspect, shaft (just sternal to cotyla scapularis) more rounded in cross-section; tibiotarsus—condylus medialis and condylus lateralis short and wide, epicondylus medialis large; tarsometatarsus—distal half of facies dorsalis convex rather than concave, tuberculum intercondylarum small, tuberositas musculo tibialis cranialis large and protruding dorsad to facies dorsalis, fossa metatarsi large and deep, extending beyond medial edge of facies dorsalis; pedal digit I, phalanx 1—large size, straight shaft; pedal digit II–IV, terminal phalanx—large size, dorso-ventrally compressed, medio-laterally expanded.

Genus *Megapodius*

Within the Megapodiidae, the fossils are referred to *Megapodius* (including *Eulipoa*, following Ripley 1960) rather than to *Leipoa, Alectura, Aepypodius, Tallegalla,* or *Macrocephalon* by the following combination of characters: tibiotarsus—distal margin of pons supratendineus nearly perpendicular (less diagonal) to the long axis of the shaft, ventral margin of condylus lateralis protrudes more ventrad from the shaft; tarsometatarsus—shaft wide but dorso-ventrally compressed, fossa metatarsi I distinct, deep, and circular in deeper portion, foramen vasculare distale large; pedal digit II–IV, terminal phalanx—dorso-ventrally compressed, medio-laterally expanded.

Megapodius alimentum, new species
Figs. 1–3

Holotype.—Distal end of tibiotarsus, BPBM 165686, Pit 0N0W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Paratypes.—All from Tongoleleka site. Proximal end of tarsometatarsus, BPBM 165689, Pit 0N0W, Layer IV (CU-III). Tarsometatarsus lacking both ends, BPBM 165670, Pit 45N1W, Layer IV (CU-III).

Fig. 2. The tarsometatarsus of *Megapodius* in dorsal (A–D) and plantar (E–H) aspects. A, E, Holotype of *M. molistructor,* New Caledonia, MNHN 600; B, F, Paratypes of *M. alimentum,* new species, Lifuka, Tonga, BPBM 165689, 165670; C, G, *M. freycinet freycinet,* male, Halmahera, Northern Moluccas, USNM 557015; D, H, *M. pritchardi,* sex unknown, Niuafo`ou, Tonga, USNM 319633. Scale bar = 10 mm.

Pedal digit I, phalanx 1, BPBM 165674, Pit 0N11W, Layer IV pit (CU-III). Pedal digit II–IV (exact number uncertain), terminal phalanx, BPBM 165675, Pit 0N11W, Layer IV pit (CU-III).

Diagnosis.—A large species of *Megapodius,* exceeded in size only by *M. molistructor* (Tables 1–3). *Megapodius alimentum* differs from *M. freycinet* as follows: tibiotarsus—incisura intercondylaris wider, tuberositas retinaculi musculo fibularis larger and more distinctly offset from condylus lateralis; tarsometatarsus—foramina vascularia proximalia more deeply inset below the dorsal surface of facies dorsalis, lateral margin of facies dorsalis more rounded at level of foramina vascularia proximalia; digit I, phalanx 1—stouter; digit II–IV, terminal phalanx—broader medio-laterally. *Megapodius alimentum* differs from *M. molistructor* in the same characters of the tarsometatarsus, as well as in the smaller foramina vascularia proximalia and the less prominent crista plantare medialis. *Megapodius alimentum* differs from *M. pritchardi* in the same characters of the tibiotarsus and phalanges, but not those of the tarsometatarsus.

Etymology.—From the Latin *alimentum,* meaning "food." The name *alimentum* refers to the presumed eating of this species by the early Tongans who deposited the bones at Tongoleleka.

Remarks.—Although modern skeletons were not available for *Megapodius laperouse* of Micronesia (Palau, Marianas), measurements of skins (Baker 1951:106–113) indicate that *M. laperouse* is smaller than *M. freycinet freycinet,* and therefore would be significantly smaller than *M. alimentum.* In spite of their large difference in size (Tables 1–3), the qualitative similarity between the tarsometatarsi of *M. alimentum* and *M. pritchardi* suggests that the former may be more closely related to *M. pritchardi* than to *M. freycinet.*

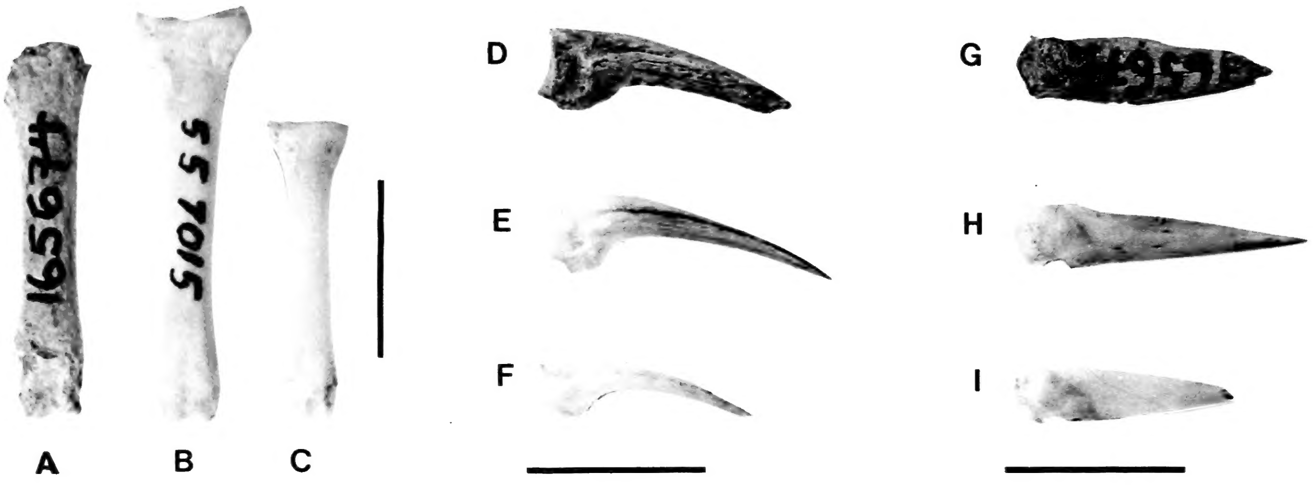


FIG. 3. The digit I, phalanx 1 in dorsal aspect (A–C) and digit II–IV (exact number uncertain), terminal phalanx in lateral (D–F) and ventral (G–I) aspects in *Megapodius*. A, Paratype of *M. alimentum,* new species, Lifuka, Tonga, BPBM 165674; D, G, Paratype of *M. alimentum,* new species, Lifuka, Tonga, BPBM 165675; B, E, H, *M. freycinet freycinet,* male, Halmahera, Northern Moluccas, USNM 557015; C, F, I, *M. pritchardi,* sex unknown, Niuafo'ou, Tonga, USNM 319633. Scale bars = 10 mm.

Megapodius cf. *molistructor*
Balouet & Olson
Fig. 4

Referred material.—Humeral half of coracoid, lacking most of processus acrocoracoideus, facies articularis clavicularis, and processus coracoideus, BPBM 165682, Pit 0N11W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Ha'apai Group, Tonga. Tom Dye and field party Aug 1984.

Table 1.—Measurements (in mm) of the tibiotarsus in *Megapodius,* giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. F = female. M = male. U = sex unknown.

	Least width of shaft	Least depth of shaft	Distal width through condyles	Distal width through epicondylus medialis	Depth of condylus lateralis	Length through pons supratendineus	Width of incisura intercondylaris
Megapodius alimentum	5.5	4.8	12.2	12.8	10.5	3.0	2.7
Holotype, BPBM 165686	1	1	1	1	1	1	1
Lifuka, Tonga (U)							
M. pritchardi	3.9	3.4	8.2	8.3	7.3	1.8	2.0
Niuafo'ou, Tonga (2U)	3.8–4.0	3.3–3.5	8.1–8.3	8.1–8.5	7.1–7.5	1.6–2.0	1.9–2.0
	2	2	2	2	2	2	2
M. freycinet freycinet	5.60	4.35	11.30	11.75	9.40	2.65	2.10
Halmahera, Moluccas	4.8–6.4	3.7–4.7	10.3–12.2	11.1–12.5	8.8–10.1	2.0–3.2	1.5–2.6
(12M, 10F)	22	22	21	21	20	22	19
M. freycinet pusillus	5.9	4.6	12.3	12.6	9.9	2.6	2.6
Philippines (M)	1	1	1	1	1	1	1
M. freycinet gilberti	4.6	3.8	9.4	9.6	8.2	2.2	1.6
Celebes (1M, 1F)	4.3–5.0	3.7–3.8	9.1–9.6	9.6–9.7	8.1–8.3	2.2	1.4–1.7
	2	2	2	2	2	2	2
M. freycinet abbotti	5.6	4.6	11.4	11.7	9.9	2.7	2.3
Nicobar Islands (2M)	5.3–5.9	4.5–4.7	11.3–11.6	11.3–12.1	1	2.5–2.9	2.2–2.4
	2	2	2	2		2	2

Table 2.—Measurements (in mm) of the tarsometatarsus in *Megapodius,* giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. The values for *M. molistructor* are estimations extrapolated from similar measurements in Table 3 of Balouet & Olson (in press b). FVP = foramina vascularia proximalia. F = female. M = male. U = sex unknown.

	Proximal depth to hypotarsal canal	Depth of lateral side of facies dorsalis at level of FVP	Width of shaft at proximal edge of fossa metatarsi I	Minimum width of shaft through fossa metatarsi I	Depth of shaft just proximal to fossa metatarsi I	Length of fossa metatarsi I
Megapodius alimentum	7.0	3.4	6.7	6.6	3.7	9.5
Lifuka, Tonga (U)	1	1	1	1	1	1
BPBM 165670, 165689						
M. pritchardi	4.4	1.9	4.2	4.3	2.4	5.9
Niuafo'ou, Tonga (2U)	4.3–4.4	1.8–2.0	4.2–4.3	4.2–4.4	2.3–2.5	5.6–6.2
	2	2	2	2	2	2
M. molistructor	ca. 7.7	—	ca. 8.7	ca. 8.9	ca. 4.4	—
New Caledonia (U)	1		1	1	1	
M. freycinet freycinet	5.80	2.45	6.10	6.25	3.25	8.85
Halmahera, Moluccas	4.8–6.3	1.7–2.9	5.5–6.8	5.6–7.0	2.9–3.6	7.9–9.6
(12M, 10F)	19	20	22	22	22	22
M. freycinet pusillus	6.2	2.6	6.4	6.7	3.5	9.6
Philippines (1M)	1	1	1	1	1	1
M. freycinet gilberti	4.8	2.4	5.0	5.2	2.7	7.9
Celebes (1M, 1F)	4.8	2.0–2.7	4.9–5.0	5.1–5.3	2.6–2.8	7.8–8.0
	2	2	2	2	2	2
M. freycinet abbotti	5.8	2.4	6.4	6.5	3.2	9.0
Nicobar Islands (2M)	5.8–5.9	1	6.2–6.5	6.2–6.8	3.1–3.4	8.7–9.2
	2		2	2	2	2

Table 3.—Measurements (in mm) of the digit I, phalanx 1 (DI, P1) and digit II–IV, terminal phalanx (DII–IV, TP) in *Megapodius,* giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. F = female. M = male. U = sex unknown.

	Length of DI, P1	Minimum width of DI, P1	Minimum depth of DI, P1	Maximum width of DII–IV, TP
Megapodius alimentum	21.2+	3.0	2.9	4.0+
Lifuka, Tonga (U)	1	1	1	1
BPBM 165674, 165675				
M. pritchardi	16.3	2.0	1.6	2.7
Niuafo'ou, Tonga (2U)	16.0–16.6	1.9–2.0	1.6–1.7	2.6–2.8
	2	2	2	2
M. freycinet freycinet	22.25	2.55	2.55	3.20
Halmahera, Moluccas	20.8–23.9	2.2–2.8	2.3–2.8	2.7–3.5
(12M, 10F)	21	22	22	22
M. freycinet pusillus	23.2	2.6	2.4	3.0
Philippines (1M)	1	1	1	1
M. freycinet gilberti	18.8	2.0	2.0	2.4
Celebes (1M, 1F)	18.3–19.3	1.9–2.1	1.9–2.0	1
	2	2	2	
M. freycinet abbotti	21.5	2.5	2.4	3.2
Nicobar Islands (2M)	21.5	2.5	2.3–2.4	3.0–3.5
	2	2	2	2

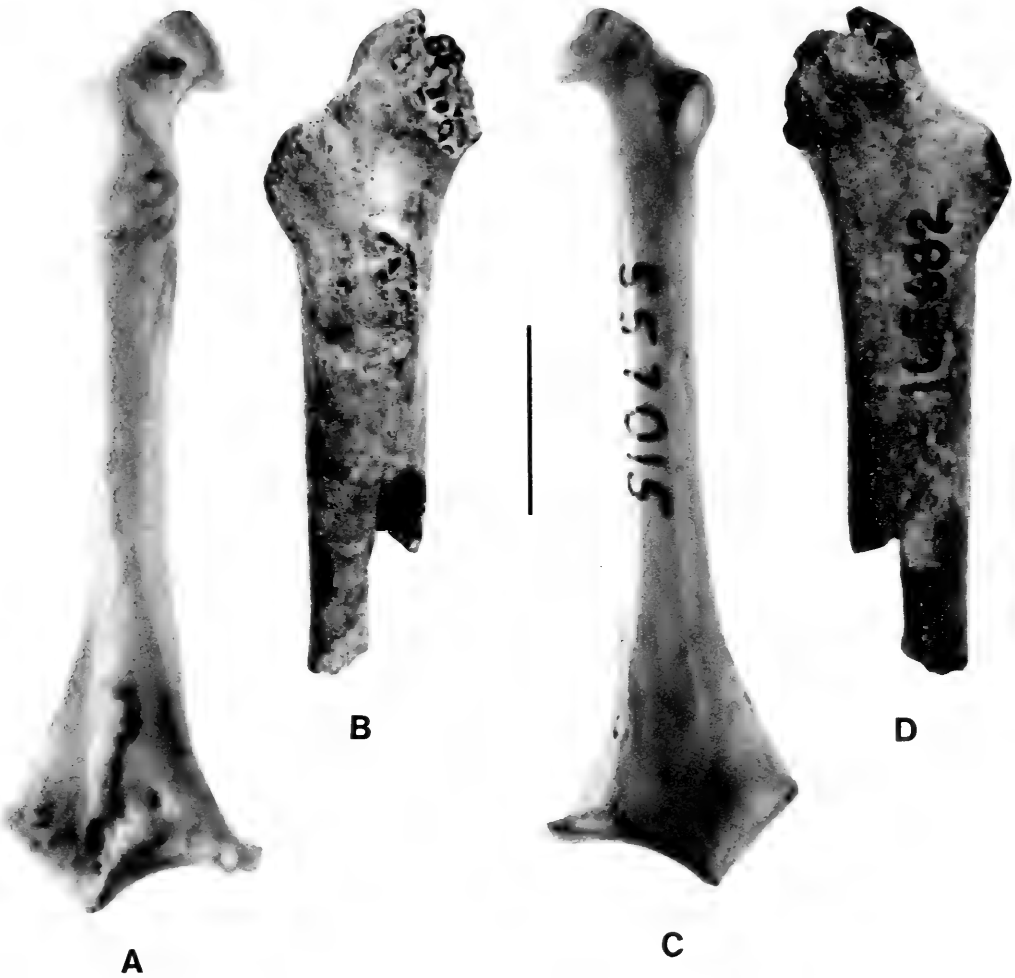


Fig. 4. The coracoid of *Megapodius* in dorsal (A, B) and ventral (C, D) aspects. A, C, *M. freycinet freycinet,* male, Halmahera, Northern Moluccas, USNM 557015; B, D, *M. molistructor,* Lifuka, Tonga, BPBM 165682. Scale bar = 10 mm.

Remarks.—This specimen is referred to *Megapodius molistructor* on the basis of its being much larger than any other species of *Megapodius* (Table 4), which is the only genus of Megapodiidae that occurs in Oceania. Intergeneric comparisons were not made. BPBM 165682 differs further from the coracoids of *M. pritchardi, M. freycinet,* and *M. wallacei* in having a less concave facies articularis humeralis. Although additional material is needed to determine with certainty whether the coracoid from Lifuka is conspecific with that of *M. molistructor,* this specimen does demonstrate that an extremely large species of megapode, approximately the size of *M. molistructor,* once lived on Lifuka.

The type series of *Megapodius molistructor,* an extinct species known otherwise only from New Caledonia (Balouet & Olson, 1989), does not include a coracoid. Nevertheless, BPBM 165682 is much larger than in *M. freycinet* and larger than would be expected for the coracoid of *M. alimentum.* In coracoidal measurements (Table 4), *M.* cf. *molistructor* from Lifuka is from 1.30+ to 1.45 times larger ($\bar{x}$ = 1.35+, n = 5) than the means for *M. freycinet freycinet.* This corresponds with ratios of the measurements of the scapula and ulna from the type series of *M. molistructor,* which are from 1.25 to 1.40 times larger ($\bar{x}$ = 1.33, n = 7) than the means for *M. freycinet freycinet* (Balouet & Olson, 1989:Table 3). No leg elements of *M.* cf. *molistructor* are available from Lifuka. The tarsometatarsus in *M. molistructor* from New Caledonia is much more massive than in *M. alimentum*

Table 4.—Measurements (in mm) of the coracoid in *Megapodius,* giving mean, range, and sample size. For sample sizes larger than 10, the mean is rounded to the nearest 0.05. CS = cotyla scapularis. FAC = facies articularis clavicularis. FAH = facies articularis humeralis. ILA = impressio ligamentum acrocoracoideum. F = female. M = male. U = sex unknown.

	Depth of FAC	Depth between ILA & FAH	Width of FAH	Length of FAH & CS	Minimum width of shaft
M. pritchardi	4.1	2.4	3.8	7.8	3.0
Niuafoʻou, Tonga (2U)	4.0–4.2	2.2–2.5	3.6–4.0	7.6–7.9	2.9–3.1
	2	2	2	2	2
M. cf. *molistructor*	7.9+	4.2	6.3+	13.6	5.7
BPBM 165682	1	1	1	1	1
Lifuka, Tonga (U)					
M. freycinet freycinet	5.95	2.90	4.85	10.20	4.20
Halmahera, Moluccas	5.4–6.4	2.6–3.4	4.6–5.2	9.5–11.2	3.6–4.6
(8M, 8F)	16	16	16	16	16
M. freycinet pusillus	6.4	2.9	4.8	10.3	4.5
Philippines (M)	1	1	1	1	1
M. freycinet gilberti	5.9	2.6	4.3	9.2	3.8
Celebes (1M, 1F)	5.6–6.2	2.4–2.7	1	9.1–9.2	3.8–3.9
	2	2		2	2
M. freycinet abbotti	6.2	3.0	4.8	10.1	4.2
Nicobar Islands (2M)	6.0–6.3	2.8–3.1	1	1	4.1–4.4
	2	2			2
M. wallacei	5.6	2.7	4.5	9.6	3.7
Halmahera, Moluccas (M)	1	1	1	1	1

(Fig. 2). Measurements of the tibiotarsus and tarsometatarsus of *M. alimentum* from Lifuka are, respectively, from 0.98 to 1.21 times larger ($\bar{x}$ = 1.10, n = 7) and 1.05 to 1.39 times larger ($\bar{x}$ = 1.16, n = 6) than the means for *M. freycinet freycinet,* while measurements of the femur and tarsometatarsus of *M. molistructor* from New Caledonia are, respectively, from 1.32 to 1.54 times larger ($\bar{x}$ = 1.39, n = 3) and 1.14 to 1.43 times larger ($\bar{x}$ = 1.31, n = 4) than the mean values for *M. freycinet freycinet.* The validity of these calculations is not likely to be compromised by a sexual dimorphism in size, which is extremely slight or non-existent in species of *Megapodius* (Mayr 1938, Amadon 1942).

Order Columbiformes
Family Columbidae
Genus *Ducula*

Two specimens are referred to the genus *Ducula* rather than other genera of pigeons from Polynesia or eastern Melanesia (*Columba, Ptilinopus, Caloenas, Gallicolumba, Goura, Didunculus*) because of these characters: coracoid—medio-ventral side of humeral end of shaft rounded, sulcus musculo supracoracoidei smooth and shallow, facies articularis sternalis medio-laterally expanded but dorso-ventrally compressed, impressio musculo sternocoracoidei deepest in medio-sternal corner; tibiotarsus—size and placement of prominent muscle scar on medio-distal surface of shaft, degree of concavity on the distal portion of shaft.

Ducula, undescribed species
Fig. 5

Material.—Tibiotarsus lacking both ends, BPBM 165685, Pit 0N0W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Haʻapai Group, Tonga. Tom Dye and field party Aug 1984.

Remarks.—This tibiotarsus is larger than in any other species of *Ducula* (Table 5).

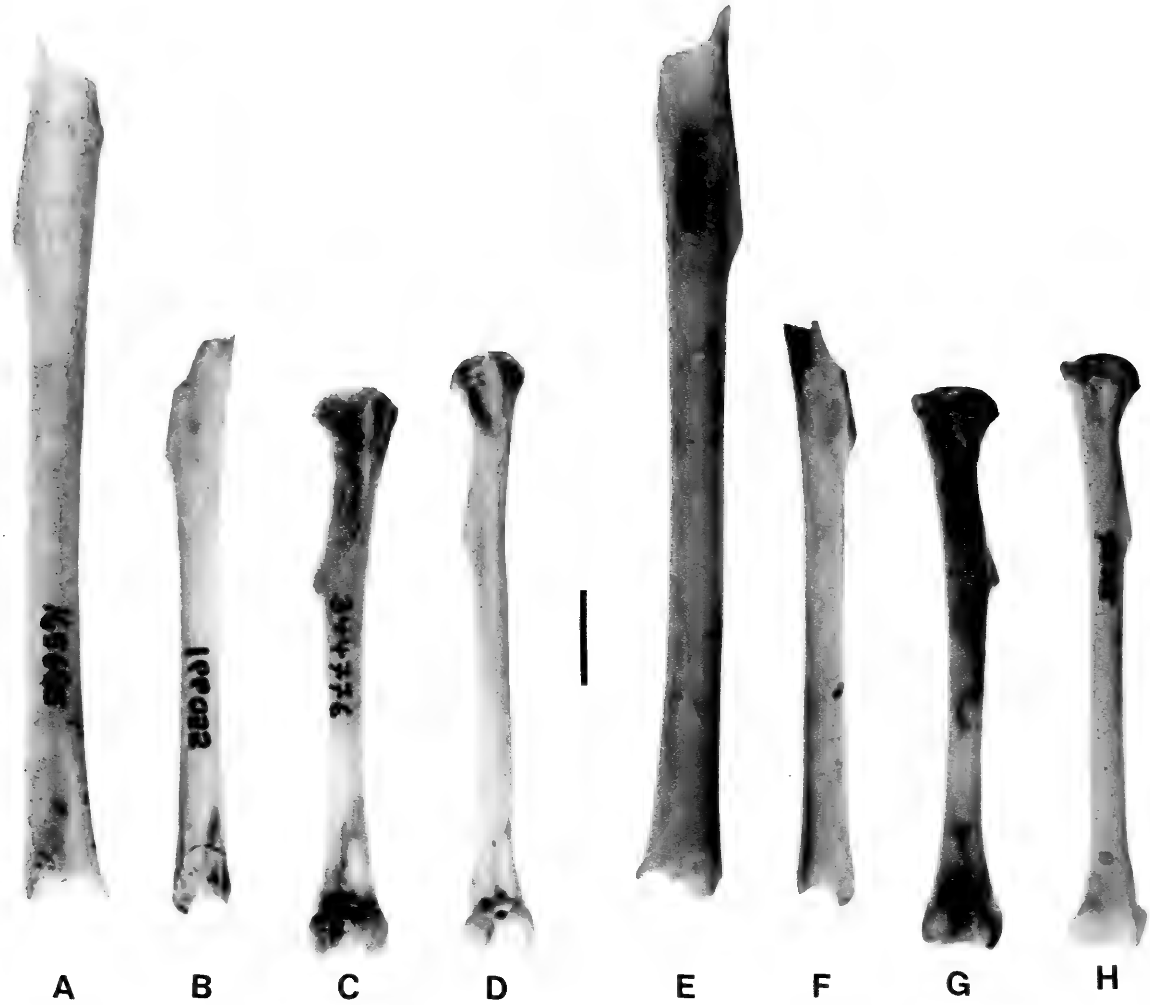


Fig. 5. The tibiotarsus of *Ducula* in cranial (A–D) and caudal (E–H) aspects. A, E, Undescribed species, Lifuka, Tonga, BPBM 165685; B, F, *D. galeata,* Hanatekua Shelter No. 2 Archeological Site, Hiva Oa, Marquesas, BPBM 166055; C, G, *D. aurorae,* male, captive (original stock presumably from Makatea Island, Tuamotus), USNM 344776; D, H, *D. pacifica,* male, Rarotonga, Cook Islands, USNM 559586. Scale bar = 10 mm.

The proximo-ventral and disto-lateral portions of the shaft have smoother, more rounded surfaces than other species. This tibiotarsus is too fragmentary to be named, yet it represents one of the largest of all columbids, being exceeded in size only by the crowned pigeons of New Guinea (*Goura* spp.).

Ducula cf. *david* Balouet & Olson
Fig. 6

Referred material.—Nearly complete coracoid, lacking processus acrocoracoideus and part of facies articularis clavicularis, BPBM 165692, Pit 0N0W, Layer IV (CU-III), Tongoleleka archeological site (To-Li), Lifuka, Ha`apai Group, Tonga. Tom Dye and field party Aug 1984.

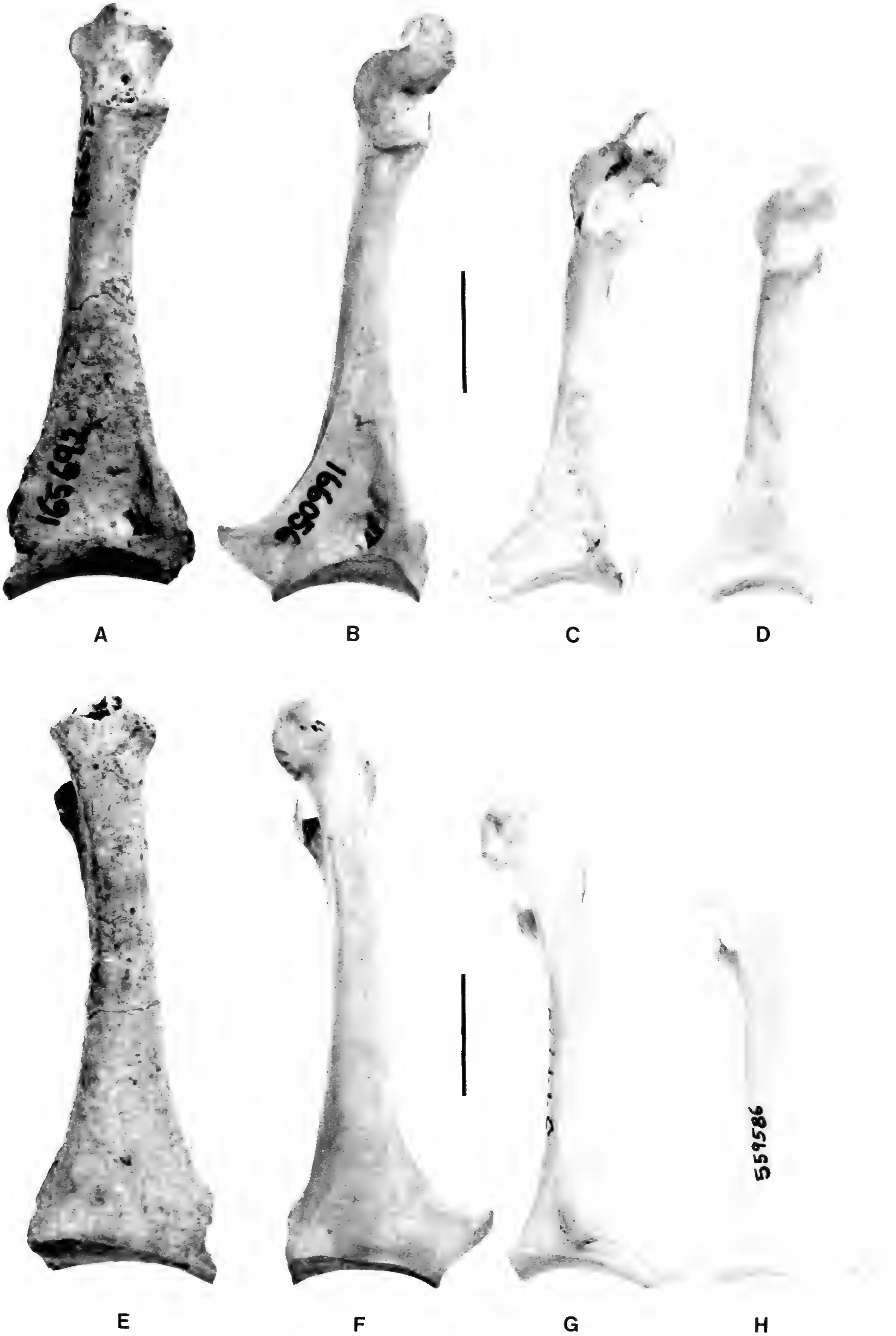
Remarks.—*Ducula david,* recently described from Wallis Island, was characterized mainly by being larger than any extant congeners (Balouet & Olson, 1987). Among living species of *Ducula,* the largest of which occurs on oceanic islands, only *D. galeata* of eastern Polynesia and *D. goliath* of New Caledonia approach the size of *D. david,* although even these species are slightly smaller and less robust (Table 6).

Ducula david is exceeded in size only by the huge extinct species noted above. Although comparable elements are not available for the undescribed species and *D. david,* comparisons of measurements of these

Table 5.—Measurements (in mm) of the tibiotarsus in *Ducula* and *Goura,* giving mean, range, and sample size. F = female. M = male. U = unknown.

	Length from distal end of fibular crest to distal knob	Length of fibular crest	Least width of shaft	Least depth of shaft
Ducula, undescribed sp.	57.4	23.3	5.5	4.8
Lifuka, Tonga (U)	1	1	1	1
D. galeata	39.7+	—	3.9	3.3
Nuku Hiva, Marquesas (M)	(est. 41–42)		1	1
	1			
D. galeata	40.5	—	4.3	3.3
Henderson Island (U)	(composite)		1	1
BPBM 160464, 160267				
D. galeata	41.5	—	4.2	3.6
Hiva Oa, Marquesas (U)	1		1	1
BPBM 166055				
D. goliath	27.1	12.7	4.3	3.8
New Caledonia (1M, 2F)	26.2–28.1	11.7–13.6	4.1–4.7	3.6–4.1
	3	3	3	3
D. aurorae	26.6	10.9	3.9	3.0
Captive (M)	1	1	1	1
D. pacifica	30.9	11.0	3.6	2.9
Niuafoʻou, Rarotonga	30.2–31.8	10.9–11.2	3.3–3.7	2.8–3.0
(1M, 1F, 1U)	3	3	3	3
D. oceanica	30.0	11.2	3.0	2.5
Palau, Ponape (2U)	28.5–31.4	11.0–11.4	3.0–3.1	2.4–2.6
	2	2	2	2
D. aenea	28.4	14.2	4.1	3.3
Philippines (F)	1	1	1	1
D. perspicillata	28.9	13.6	3.9	3.2
Halmahera, Moluccas	28.2–29.6	13.2–14.1	3.9	3.0–3.4
(1M, 1F)	2	2	2	2
D. bicolor	38.5	13.0	3.7	3.0
Halmahera, Moluccas (M)	1	1	1	1
D. luctuosa	28.2	13.9	3.5	3.1
Celebes (F)	1	1	1	1
D. spilorrhoa	25.2	14.2	3.2	2.9
Australia (U)	1	1	1	1
D. badia	23.1	13.1	3.4	2.8
Thailand (M)	1	1	1	1
D. pinon	29.4	14.0	4.0	3.1
Captive (M)	1	1	1	1
D. radiata	19.4	10.7	3.1	2.4
Celebes (M)	1	1	1	1
Goura victoria	68.0	24.7	6.7	5.9
Captive (M)	1	1	1	1

species with those of *D. galeata* and *D. goliath* indicate that the undescribed species is larger than *D. david* (Tables 5 and 6 herein; Balouet & Olson, 1987: Table 1). In particular, the tibiotarsus of the undescribed species is 1.40 times longer than that of *D. galeata,* whereas the holotypical tarsometatarsus of *D. david* from Wallis Island is only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1.01 times longer than that of *D. galeata* and 1.12 times longer than that of *D. goliath.* These ratios correspond well with those of the coracoid in *D.* cf. *david* from Lifuka, which is 1.07 times longer than that in *D. galeata* and 1.12 times longer than that in *D. goliath.* The amount of sexual dimorphism in size is poorly understood in oceanic species of *Ducula* owing to the worldwide scarcity of skeletons. In measurements of *D. goliath,* the male is consistently larger than the female (Tables 5 and 6), although these are captive individuals that may not be reliable indicators of the size of wild birds.

No skeletons were available for *D. latrans* of Fiji. Based upon measurements of skins (duPont 1976:83–85), *D. latrans* is approximately the same size as *D. aurorae* or *D. pacifica,* and thus would be much smaller than *D. david.*

Ducula pacifica (Gmelin)

Referred material.—Ulna lacking both ends (BPBM 165676), Pit 126N0W, Layer III (CU-IIb), Tongoleleka archeological site (To-Li), Lifuka, Ha`apai Group, Tonga. Tom Dye and field party Aug 1984.

Remarks.—The curvature of the shaft and the prominent papillae remigiales caudales refer this ulna to the Columbidae. The specimen agrees in size and other features with the ulna of *Ducula pacifica.* Each of the other three species of columbids reported here is much larger than *D. pacifica,* which is the only species of columbid (other than *Gallicolumba stairii* and species of *Ptilinopus,* which are very small) surviving on Lifuka or anywhere else in Tonga.

Genus *Caloenas*

Among the bird bones from the Tongoleleka Site is another coracoid of a large columbid. This specimen, slightly smaller than in *D.* cf. *david* (Table 6), is referred to the genus *Caloenas* rather than to *Ducula* or other pertinent genera of columbids because of these characters: greater pneumaticity in humeral end of sulcus musculo supracoracoidei; facies articularis humeralis protrudes more ventrad from surface of shaft; sharp medio-ventral edge of humeral end of shaft; in medial aspect, portion of shaft between cotyla scapularis and facies articularis clavicularis faces more perpendicularly (less diagonally); facies articularis clavicularis deeper.

Caloenas cf. *canacorum* Balouet & Olson
Fig. 7

Referred material.—Humeral end of coracoid, including facies articularis humeralis and cotyla scapularis, BPBM 165678, Pit 0N20E, Layer II (CU-II), Tongoleleka archeological site (To-Li), Lifuka, Ha`apai Group, Tonga. Tom Dye and field party Aug 1984.

Remarks.—*Caloenas canacorum* is an extinct species recently described from late Holocene fossils (sternum, coracoids, scapula, and humerus) from New Caledonia (Balouet & Olson, 1989). Although direct comparison of the holotype coracoid of *C. canacorum* with BPBM 165678 was not possible except in photographs (Fig. 7), BPBM 165678 is referred to *C.* cf. *canacorum* because of similarity in qualitative generic characters and in size, being significantly larger than in *C. nicobarica,* the only living species in this distinctive genus (Table 6).

Discussion

Although the detailed implications of these findings will be reported elsewhere, a

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Fig. 6. The coracoid of *Ducula* in dorsal (A–D) and ventral (E–H) aspects. A, E, *D.* cf. *david,* Lifuka, Tonga, BPBM 165692; B, F, *D. galeata,* Hanatekua Shelter No. 2 archeological site, Hiva Oa, Marquesas, BPBM 166056; C, G, *D. aurorae,* male, captive (original stock presumably from Makatea Island, Tuamotus), USNM 344776; D, H, *D. pacifica,* male, Rarotonga, Cook Islands, USNM 559586. Scale bars = 10 mm.

Table 6.—Measurements (in mm) of the coracoid in *Ducula* and *Caloenas,* giving mean, range, and sample size. The values for *D. david* from Wallis Island are estimations extrapolated from similar measurements in Table 1 of Balouet & Olson (1987). The values for *C. canacorum* from New Caledonia are taken, either directly or from extrapolated estimations, from Balouet & Olson (1989). F = female. M = male. U = sex unknown.

	Maximum length	Length from sternal facet to sternal end of facies articularis humeralis	Depth of humeral end	Length of facies articularis humeralis	Width of facies articularis humeralis	Least depth of shaft between cotyla scapularis and processus acrocoracoideus	Least depth of shaft	Least width of shaft	Width of sternal end
D. cf. *david* Lifuka, Tonga (U)	48.0+ (est. 53) 1	41.8 1	—	—	5.5+ 1	6.9 1	4.9 1	5.1 1	15.5+ (est. 21) 1
D. david Wallis Island (U)	—	—	—	—	—	—	ca. 4.2 1	—	—
D. galeata Hiva Oa, Marquesas BPBM 166056 (U)	49.6 1	38.2 1	5.6 1	7.6 7.1–8.0 2	4.3 4.0–4.6 2	5.0 4.9–5.2 2	3.9 1	3.8 1	18.0 1
D. goliath New Caledonia (1M, 2F)	47.6 44.9–49.6 3	35.8 34.1–37.4 3	6.1 5.5–6.5 3	7.2 6.9–7.4 2	4.8 4.3–5.4 2	5.3 5.0–5.6 2	4.2 4.0–4.7 3	4.4 4.1–4.8 3	18.7 17.4–20.1 3
D. aurorae Captive (M)	41.2 1	31.1 1	4.6 1	6.2 1	4.0 1	—	3.6 1	3.7 1	15.3 1
D. pacifica Gilberts, Niuafo‘ou, Rarotonga (2M, 1F, 1U)	37.8 36.3–41.0 4	29.4 28.4–32.2 4	4.0 3.9–4.1 4	5.5 5.3–5.9 4	3.6 3.2–3.9 4	3.9 3.5–4.3 4	2.8 2.5–3.0 4	2.8 2.4–3.1 4	14.2 13.4–15.6 4
D. oceanica Palau, Ponape (3U)	34.9 32.7–36.5 3	27.0 25.1–28.2 3	3.8 3.5–4.0 3	4.7 4.5–5.0 3	3.1 3.0–3.3 3	3.6 3.6–3.7 2	2.8 2.6–3.0 3	2.6 2.4–2.8 3	13.6 13.4–13.8 2
D. myristicivora Captive (M)	47.8 1	34.9 1	5.7 1	8.0 1	—	—	4.0 1	4.2 1	—
D. aenea Philippines (F)	45.2 1	34.1 1	4.7 1	7.6 1	4.0 1	5.0 1	4.0 1	3.8 1	17.3 1
D. perspicillata Halmahera, Moluccas (1M, 1F)	46.6 45.9–47.2 2	35.0 34.4–35.5 2	5.4 5.2–5.5 2	7.6 7.2–8.1 2	4.4 4.4–4.5 2	4.8 4.7–5.0 2	4.0 3.8–4.2 2	4.0 3.9–4.1 2	18.5 18.4–18.6 2

Table 6.—Continued.

	Maximum length	Length from sternal facet to sternal end of facies articularis humeralis	Depth of humeral end	Length of facies articularis humeralis	Width of facies articularis humeralis	Least depth of shaft between cotyla scapularis and processus acrocoracoideus	Least depth of shaft	Least width of shaft	Width of sternal end
D. bicolor	41.5	31.0	4.5	7.2	4.0	4.6	3.6	3.5	—
Halmahera, Moluccas (M)	1	1	1	1	1	1	1	1	
D. luctuosa	43.0	33.0	5.0	7.1	4.1	—	3.7	3.8	—
Celebes (F)	1	1	1	1	1		1	1	
D. spilorrhoa	40.7	30.5	4.8	7.0	4.0	—	3.7	3.8	—
Australia (U)	1	1	1	1	1		1	1	
D. badia	42.9	32.6	4.5	6.3	3.9	—	3.5	3.8	—
Thailand (M)	1	1	1	1	1		1	1	
D. pinon	48.6	36.7	5.4	7.0	4.5	—	4.0	3.9	—
Captive (M)	1	1	1	1	1		1	1	
D. radiata	38.9	29.3	3.8	6.0	3.0	3.6	2.9	2.9	14.4
Celebes (M)	1	1	1	1	1	1	1	1	1
Caloenas nicobarica	44.8	33.7	5.1	7.4	4.7	5.1	3.6	3.6	15.8
Halmahera, Moluccas	43.5–46.5	32.3–34.8	4.8–5.5	6.8–7.9	4.4–5.0	4.6–5.5	3.3–3.8	3.2–4.0	14.9–16.8
(5F)	5	5	5	5	5	5	5	5	5
C. canacorum	59.2	—	8.2	—	—	—	—	—	—
New Caledonia (2U)	59.0–59.4		7.2–9.1						
	2		2						
C. cf. *canacorum*	—	—	6.5+	8.9	5.2	6.1	—	—	—
Lifuka, Tonga (U)			1	1	1	1			
BPBM 165678									

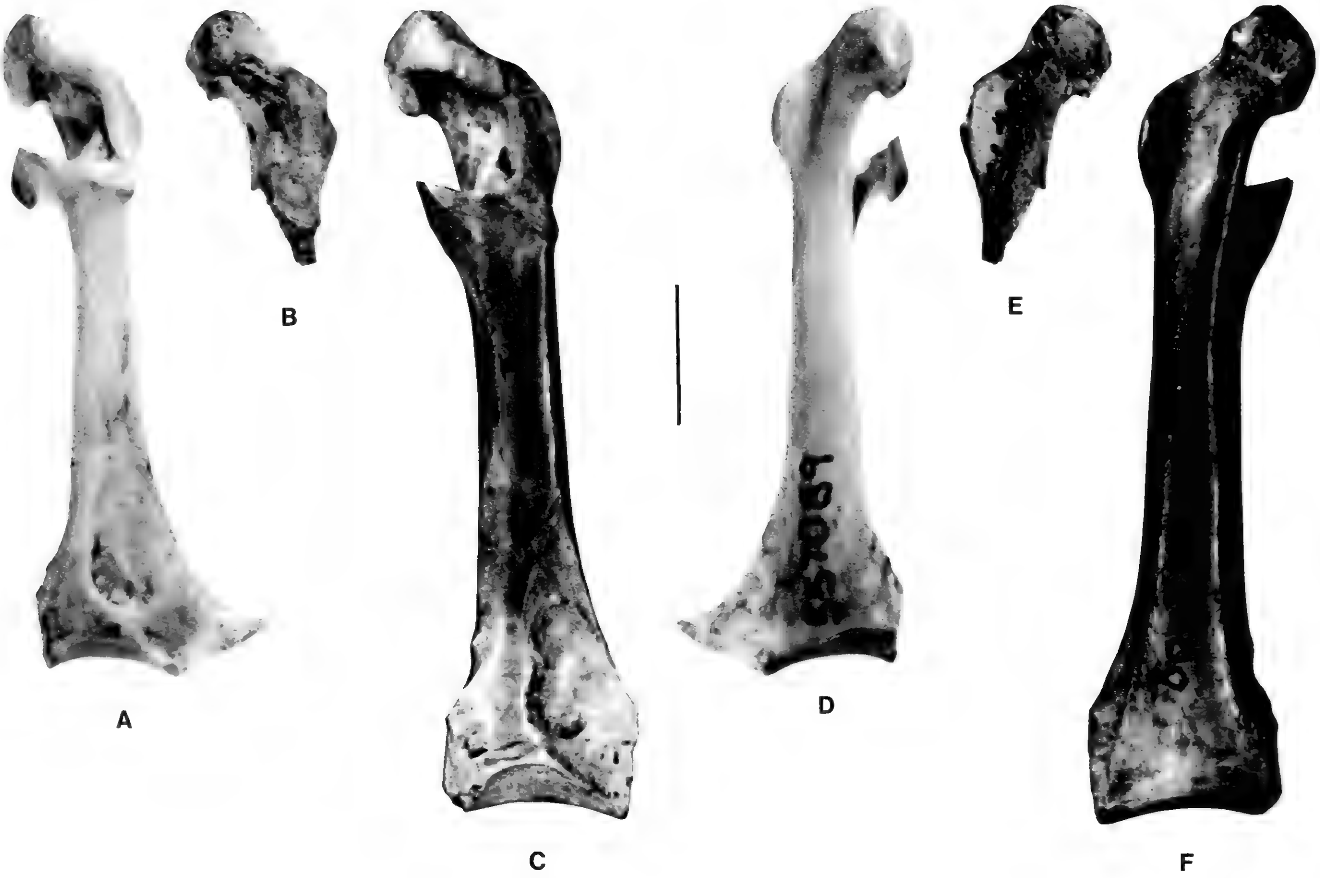

Fig. 7. The coracoid of *Caloenas* in dorsal (A–C) and ventral (D–F) aspects. A, D, *C. nicobarica,* female, Halmahera, Northern Moluccas, USNM 557089; B, E, *Caloenas* cf. *canacorum,* Lifuka, Tonga, BPBM 165678; C, F, *C. canacorum,* paratype, New Caledonia, MNHN 300. Scale bar = 10 mm.

few comments are pertinent here. The undescribed species of *Ducula* is of unknown interspecific relationships. The other extinct birds from Lifuka are related to species found west or north of Tonga. It seems likely that all of these species, or closely related ones, once occurred through much of the region of New Caledonia, Vanuatu, Fiji, Tonga, and Samoa. *Megapodius molistructor* and *Caloenas canacorum* are known only from New Caledonia and tentatively from Lifuka. *Megapodius alimentum* and the undescribed species of *Ducula* are known only from Lifuka, although there is no reason to believe that they were confined to that island. Aside from Lifuka, *D. david* is known from Wallis (Uvea) Island, which is north of Lifuka, between Samoa and Fiji.

The late Holocene extinction of two species of megapodes and three species of pigeons on Lifuka shows that there has been a significant loss of birds in western Polynesia since the arrival of man. Numerous extinctions have been documented by fossil records from more remote parts of Polynesia, such as Hawaii (Olson & James 1982a, b), Marquesas (Steadman, in press), Henderson Island (Steadman & Olson 1985), Cook Islands (Steadman 1985, in press), and New Zealand (Cassels 1984). More excavation is needed in Tonga and Samoa. Based upon the limited record available, the degree of avian extinction in western Polynesia may have been just as severe as that from elsewhere in Polynesia.

The fossils from Lifuka indicate that two species of *Megapodius* once occurred there. *Megapodius pritchardi,* restricted to the isolated Tongan island of Niuafo`ou, is the only species of megapode that survives anywhere in Polynesia, although we presently do not know to what extent the natural range of megapodes has been reduced by human impact. The widespread *M. freycinet* reaches the eastern limit of its range in Vanuatu (New Hebrides). That the absence of megapodes in the Fijian region may be an artifact of human disturbance was noted by Olson (1980) and confirmed several years ago by our examination of bones of *Megapodius* (species undetermined) from an archeological site on Lakeba, Lau Group, Fiji (reported in Gibbons & Clunie 1986). Elsewhere in the western Polynesian and Melanesian region, extinct megapodes (species undetermined) have been reported from as yet unconfirmed historical accounts in the Kermadec Islands (Lister 1911), archeological sites on Tikopia (Kirch & Yen 1982: 282; Green 1976), an egg collected in 1847 from Samoa (island undetermined; Gray 1862), and an egg collected before 1862 from an undetermined island in the Ha'apai Group of Tonga (Gray 1862, 1864). Oates (1901) referred the last two specimens to *M. pritchardi,* a determination that should be reconfirmed.

A better understanding of the systematics and natural distribution of megapodes in Oceania depends upon the reexamination of historic specimens and documents, and more fully upon the discovery and study of bones from prehistoric sites on many additional islands. It now seems likely that one to three species of megapode occurred on most or all islands of eastern Melanesia and western Polynesia before the arrival of humans. Four species of megapodes still exist, for example, on the Papuan island of Misool (Ripley 1960).

Columbids also have suffered much extinction in Oceania. The hunting of pigeons by prehistoric Tongans was extensive and highly organized (McKern 1929:19–27). *Ducula pacifica* is the largest pigeon known historically from anywhere in Tonga, where it is found essentially throughout the group. Fossils from Tongoleleka represent three additional species of columbids, each extinct and larger than *D. pacifica.* Although it may seem remarkable that four large species of columbids, including three species of *Ducula,* once lived on Lifuka, we really do not yet know the natural (=pre-human) distribution and diversity of Pacific columbids. From Mangaia in the Cook Islands, for example, late Holocene fossils represent five species of columbids where none exists today (Steadman 1985, 1989).

Acknowledgments

I thank T. Dye for his cooperation and generosity in making available the Lifukan specimens and associated information. S. L. Olson and J. C. Balouet kindly allowed access to specimens and data on extinct birds from New Caledonia, including photographs of *Megapodius molistructor* and *Caloenas canacorum.* For access to specimens, I thank J. P. Angle, S. L. Olson, C. A. Ross, and R. L. Zusi (USNM) and A. Allison, C. H. Kishinami, and G. Wine (BPBM). D. Pahlavan, S. E. Schubel, and M. C. Zarriello assisted in other curatorial matters. D. Shideler, L. Woodward, and A. Ziegler sorted and preliminarily identified the bones. The photographs are by T. Beblowski and C. Supkis. The manuscript was improved by comments from T. Dye, N. G. Miller, S. L. Olson, and G. K. Pregill. The research was supported by National Science Foundation Grant BSR-8607535. This paper is contribution number 538 of the New York State Science Service.

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GEOGRAPHIC VARIATION IN THE YELLOW-RUMPED TANAGER (AVES: THRAUPINAE)

Robert W. Storer

Abstract.—Females and young males of the Yellow-rumped Tanager (the *icteronotus* group of the Flame-rumped Tanager, *Ramphocelus flammigerus*) from Panama to west central Colombia are grayer and less green on the back with less black on the crown than are those from Ecuador. Birds from southwestern Colombia and northeastern Ecuador are intermediate between those populations, the latter being more similar to those of the other Ecuadorean populations. The name *Ramphocelus flammigerus varians* Lafresnaye should be applied to the northern populations and *R. f. icteronotus* Bonaparte to those from Ecuador.

Yellow-rumped Tanagers (the *icteronotus* group of the Flame-rumped Tanager, *Ramphocelus flammigerus*) are widely distributed from western Panama to southwestern Ecuador (American Ornithologists' Union 1983). Wetmore et al. (1984:449) comment that "preliminary examination reveals that females and immatures from Ecuador are much greener, less brownish or gray, above than are most birds from Colombia and Panama. Thus it is possible that the Panamanian birds should take the name *varians* Lafresnaye 1847 (type locality, Buenaventura Colombia)."

To determine the correct name for the Panamanian birds, it was necessary to determine first, if there is sufficient geographic variation to recognize more than one race, and second, if so, whether the birds from near the type locality of *varians* are closer to birds from Panama or western Ecuador (the restricted type locality of *icteronotus,* Berlepsch, 1912). Should the latter situation apply, a new name would be needed for the Panamanian birds.

I examined 143 specimens of females and immature males of the Yellow-rumped Tanager for analysis. (Adult males do not vary in the deep black of the back.) Wing length (chord), tail length, and length of bill from nostril to tip of females were measured with dial calipers, the first two to the nearest 0.5 mm and the last to the nearest 0.1 mm. (The sample of males was too small to treat statistically.) The geographic range was divided into five areas with gaps between them to avoid comparisons between contiguous populations and to reduce overlap between samples. The selection of the areas was based primarily on the distribution of the material. These areas were: Western Panama (Bocas del Toro Province and the Canal Zone), Eastern Panama (Darien Province), Central Colombia (provinces of Cauca, Tolima, and Valle), Northern Ecuador (provinces of Esmeraldas, Imbabura, and Pichincha), and Southern Ecuador (provinces of Canar, El Oro, Guayas, and Loja).

Color comparisons were made by examination of specimens in north light. Badly worn or faded specimens, approximately one half of those examined, were not used in the comparisons.

The measurement data for females (Table 1) show a cline in increasing wing and tail length from western Panama to southern Ecuador. Bill length is greatest in birds from eastern Panama and least in those from western Panama and central Colombia, but mean differences are small. In none of the

Table 1.—Sample size, mean, and standard deviation of measurements of female Yellow-rumped Tanagers.

Measurement	Western Panama		Eastern Panama		Central Colombia		Northern Ecuador		Southern Ecuador	
Wing length	7	78.1 ± 3.6	9	78.9 ± 1.9	23	79.3 ± 1.8	10	80.4 ± 2.6	12	83.4 ± 1.9
Tail length	6	68.2 ± 3.2	8	68.9 ± 3.2	21	69.1 ± 2.7	10	69.7 ± 2.3	12	73.8 ± 3.7
Bill length	7	12.8 ± 0.8	9	13.4 ± 0.6	22	12.8 ± 0.6	10	13.2 ± 0.3	12	13.1 ± 0.7

measurements is the difference between the largest and smallest mean greater than the sum of the standard deviations. Therefore, none of the differences approaches a degree of difference useful in separating subspecies. In wing and tail measurements, the birds from central Colombia are closer to those from eastern Panama than to those from northern Ecuador. The data for bill length are equivocal.

In color, specimens from Panama are decidedly grayer (less black) on the back than those from Ecuador, the crowns are less black, the yellow edging on the back feathers is paler and contrasts less with the dark color of the rest of the feather, and the yellow of the underparts is paler, especially on the abdomen. The brighter yellow edgings and darker central parts of the feathers combine to produce a greener tone to the back feathers of the Ecuadorean birds. Five specimens from the province of Valle, central Colombia, (including Buenaventura, the type locality of *varians*) are nearer birds from Panama in color than those from Ecuador. In Ecuador, there is a noticeable difference in color between specimens from the northern and those from the central and southern parts of the country, the latter being brighter. However, birds from northern Ecuador are more similar to those from the south than to those from Panama and northern Colombia. Thus, birds from Panama through central Colombia (Valle) vary little in color, the major change occurring from Cauca to Ecuador, with a smaller change occurring between the northern and central parts of Ecuador.

In conclusion, differences in wing, tail, and bill lengths are not sufficient to warrant recognition of subspecies. Color differences, however, are greater than in many recognized subspecies. I therefore propose that the birds from Panama through the province of Valle, Colombia, be called *Ramphocelus flammigerus varians* Lafresnaye, those from Ecuador, *Ramphocelus flammigerus icteronotus* Bonaparte, and those from southwestern Colombia, intergrades.

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TWO OVERLOOKED HOLOTYPES OF THE HAWAIIAN FLYCATCHER *CHASIEMPIS* DESCRIBED BY LEONHARD STEJNEGER (AVES: MYIAGRINAE)

Storrs L. Olson

Abstract.—The holotypes of two of the three taxa of Elepaio (*Chasiempis*) described by Leonhard Stejneger in 1887 have been overlooked for almost a century but were located in the collections of the British Museum (Natural History) and restudied. That of *Chasiempis ridgwayi* Stejneger presents no problems as it is representative of the subspecies from the windward parts of the island of Hawaii currently known as *Chasiempis sandwichensis ridgwayi.* The holotype of *Chasiempis ibidis* Stejneger, 1887, however, is identified as being from the Oahu population and this name thus takes precedence over *Chasiempis gayi* Wilson, 1891.

In the early literature on systematics and nomenclature of the Hawaiian flycatcher known as the Elepaio, *Chasiempis sandwichensis* (Gmelin), there was considerable disagreement concerning the number of taxa and their distribution. Some proponents held out for a single species (e.g. Sclater 1885, Berlepsch & Leverkühn 1890), while others recognized as many as five or six (e.g. Stejneger 1887, Wilson 1891), with the island of origin often being completely ignored, however. It was eventually determined that the Elepaio occurred only on three of the Hawaiian islands, with the population of each island coming to be recognized under a single name: *C. sclateri* Ridgway, 1882, on Kauai; *C. gayi* Wilson, 1891, on Oahu; and *C. sandwichensis* (Gmelin, 1789) on Hawaii. These taxa are now generally regarded as subspecies of *C. sandwichensis.* Geographic variation within the island of Hawaii caused Henshaw (1902) to recognize two forms there, with the second taking the name *C. ridgwayi* Stejneger, 1887. Pratt (1979, 1980) recognized these and described a third subspecies from Hawaii, *C. s. bryani.*

Leonhard Stejneger was in the thick of the early confusion surrounding the systematics of *Chasiempis* and proposed no less than three new taxa (Stejneger 1887). The only actual specimens available to him, however, were those taken on Kauai by Valdemar Knudsen and forwarded to the Smithsonian Institution. Part of the proliferation of taxa resulted from the two distinct plumage types found on each island, now generally regarded as adult and "immature." Thus, Stejneger's name *Chasiempis dolei,* the type of which (USNM 110040) is a gray-backed adult bird from Kauai, is a pure synonym of *C. sclateri* Ridgway, 1882, the cotypes of which (USNM 41955, 41956) are brown-backed immature birds from Kauai (see Deignan 1961:460).

Stejneger's other two names, *C. ridgwayi* and *C. ibidis,* were based on a color plate published in *Ibis* (hence the latter name) by Sclater (1885). Although Stejneger attempted to forestall criticism by saying that if *C. ibidis* were not distinct from *C. sclateri* "then I can only say that the published figure of the former is worse than useless" (Stejneger 1887:88), his contemporaries nevertheless roundly excoriated him. "It is a pity that Dr. Stejneger, with so much good material before him, should think it necessary to manufacture 'new species' out of other people's figures without seeing the specimens" (Sclater 1888:143). "On the genus *Chasiempis* I would offer only one remark, and that is a word of caution to those who would, on the evidence of from a couple to half-a-dozen of specimens, or perhaps even on the evidence of a badly-coloured plate, attempt to break it up into definable 'species'" (Newton 1892:469). With the benefit of hindsight, it is fair to note that the plate in question is actually quite accurate, and that both of Stejneger's taxa based on it are now seen to be valid.

Although both figures were stated to be based on particular specimens, these have been overlooked in the general collections of the British Museum (Natural History) for nearly a century and have long gone unrecognized as types (neither is mentioned in Warren & Harrison 1971). They still exist, however, and I was able to examine and compare them with the series of *Chasiempis* in the National Museum of Natural History, Smithsonian Institution (USNM), and with a selection of specimens from the American Museum of Natural History that were in plumage comparable to that of *C. ibidis* (see Material Examined).

One of Stejneger's names was applied to "the brown and chestnut colored bird from Hawaii, *Ch. ridgwayi,* figured on plate i, Ibis, 1885" (Stejneger 1887:87). Sclater (1885:18) had mentioned two specimens collected by the *Challenger* Expedition at Hilo, Hawaii, in August, 1875, and stated that "the figure (Plate I fig. 1) has been taken from one of them." Both specimens are in nearly identical plumage but one of them (BMNH 80.11.18.445, original no. 529) is in much worse condition, with most of the feathers of the rump missing and many of the rectrices broken off, so that only one remains that has a white tip. Because the plate shows a bird with a large white rump patch and white tips on most of the rectrices, if it were drawn from a single specimen, as stated by Sclater, this would have to be BMNH 80.11.18.444 (original no. 528), which I here affirm to be the holotype of *Chasiempis ridgwayi* Stejneger (culmen, 13.1 mm; wing, 67.7; tail 54.5, tarsi not measurable). No nomenclatural problems attach to this identification, as the specimen is of known provenance and is clearly the bird from windward Hawaii currently known as *Chasiempis sandwichensis ridgwayi.*

The specimen from which Sclater's remaining figure was drawn, the type of *Chasiempis ibidis,* has a much more curious and enigmatic history. Sclater (1885:18) received the specimen, labelled "Chili," prior to 1862 from the dealer Verreaux and mistook it for some undetermined species of Tyrannidae. Thus he once listed it as "*Cnipolegus* _?" (Sclater 1862:203), an error that he later corrected to *Chasiempis sandwichensis* (Sclater 1873) after comparing the specimen with material in the Berlin Museum (Sclater 1885), where the only specimens of *Chasiempis* then were those collected on Oahu by Deppe in 1837. The same specimen was listed by Sharpe (1879) as *Chasiempis sandvicensis* (*sic*), at which time it was the only example of Elepaio in the British Museum. It is the only Elepaio from the Sclater collection *ex* Verreaux in the British Museum collections or elsewhere and is thus certainly identifiable as the holotype of *Chasiempis ibidis* Stejneger (BMNH 73.8.6.3; culmen broken; wing, 62.9 mm; tail, 59.3; tarsus, 25.1). It is in fresh, unworn plumage and agrees perfectly with the figure in Sclater's (1885) plate except that the ochraceous color at the posterior margin of the throat is somewhat darker than depicted.

Circumstantial evidence alone would suggest that this specimen came from Oahu, as most commerce then, as now, was through Honolulu. That it had been labelled "Chili" is understandable as Chile was then a dispatch point for cargo going "around the Horn" to Europe. In the Senckenberg Museum, Frankfurt, are at least five specimens of Hawaiian birds labelled as received or exchanged from Chile in 1842, the notation "Erh[halten] von Chili" having been mistaken by Banko (1979:31, 32, 80) for the collector's name. Of these, three are of the Oahu form of *Loxops virens*; the other two belong to species that show no interisland variation (*Psittirostra psittacea* and *Vestiaria coccinea*). It is uncertain who was supplying specimens from Oahu through Chile at that time, but it was very likely the same source whence Verreaux obtained the specimen of *Chasiempis* sold to Sclater.

As far as the actual characters of the holotype of *Chasiempis ibidis* are concerned, Stejneger (1887:88) was perfectly correct in describing it as differing from *C. sclateri* of Kauai, which is "much deeper and richer tawny color . . . and this color extends much further on breast, flanks, and tibiae than in *Ch. ibidis.*"

Wilson (1891) considered *C. ibidis* to have come from Oahu. The new form from Oahu that he called *Chasiempis gayi* he described as a *second* species from that island *in addition* to *C. ibidis.* Why then has the Oahu bird come to be known as *C. gayi* rather than *C. ibidis*? This results entirely from Rothschild's (1893:71) statement that the type of *C. ibidis* "agrees best with the young Hawaiian bird, so there is no doubt it really came from Hawaii." This is erroneous. Rothschild's conclusion appears to have been unduly influenced by some exceptional specimens (e.g. AMNH 607136, 607138) collected by Palmer on the Kona coast of Hawaii, the first mentioned having served as the model for the immature of *C. sandwichensis* in Rothschild's accompanying plate. These birds are much more rufescent, especially on the throat and breast, than typical immature birds from Hawaii, which are dark brownish above, with a grayish crown, and white lores and underparts. The light tawny ochraceous color of the type of *C. ibidis* is very unlike this and is matched only by specimens from Oahu. The exceptionally rufescent specimens from Hawaii are still much darker, more chestnut, above, especially on the rump, than in *C. ibidis.* Another overlooked difference is in the shape of the bill, which in birds from Oahu and Kauai appears broader and flatter than in birds from Hawaii. Although the bill in the type of *C. ibidis* is damaged and lacks the tip of the upper part, its shape agrees better with birds from Oahu than with those of Hawaii.

The holotype of *Chasiempis ibidis* is unquestionably representative of the Oahu population of Elepaio, as Wilson (1891) himself recognized. Because *Chasiempis ibidis* Stejneger, 1887, has priority over *Chasiempis gayi* Wilson, 1891, the Oahu Elepaio should now be known as *Chasiempis ibidis* or *Chasiempis sandwichensis ibidis.*

Material examined.—Chasiempis s. sandwichensis: AMNH 607118, AMNH 607125, AMNH 607136, AMNH 607138. *C. s. ridgwayi*: BMNH 80.11.18.444 (holotype), BMNH 80.11.18.445, AMNH 193362, AMNH 193366, AMNH 193368, plus about 30 USNM specimens in immature plumage. *C. ibidis*: BMNH 73.8.6.3 (holotype), AMNH 193354, AMNH 193355, AMNH 193357, AMNH 168638, AMNH 199353, AMNH 607160, USNM 301122. *C. sclateri*: AMNH 168639, AMNH 193347, AMNH 607188, AMNH 607189, AMNH 607190, AMNH 607198, USNM 41955 and 41956 (cotypes), USNM 110040 (type of *C. dolei*), USNM 110037, USNM 110038, USNM 116782, USNM 116783, USNM 493863, USNM 493864, USNM 591935, USNM 591936.

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A NEW LIZARD OF THE GENUS *LEPIDODACTYLUS* (REPTILIA: GEKKONIDAE) FROM BATAN ISLAND, PHILIPPINES

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Abstract.—A new species of *Lepidodactylus, L. balioburius,* is described from Batan Island in the northernmost archipelago of the Philippines. It is most closely related to the recently described *L. yami* from Lanyu Island, Taiwan. Morphological variation in both species is analyzed.

The herpetofauna of mountainous northern Luzon and the island groups stretching north toward Taiwan remains poorly known, despite intensive field work in other parts of the Philippines during the past 20–30 years. The Batan Island group, the northernmost archipelago in the Philippines, is of considerable zoogeographic interest since it is located almost midway between the Philippines and Taiwan (220 km north of Luzon and 200 km south of Lanyu Island, see Fig. 1). A few specimens from Batan reported in the literature perished when the Bureau of Science collection in Manila was destroyed during World War II. During May and June 1985, a multidisciplinary team of biologists, coordinated by Angel C. Alcala (Silliman University) and Charles A. Ross (Smithsonian Institution), collected on several islands in the Batan Group. Their collections contained a small series of a distinctive new species of *Lepidodactylus,* a genus unreported from the extreme northern Philippines. The new species is superficially similar to the recently described *L. yami* from Lanyu Island, Taiwan (Ota 1987).

Materials and Methods

Data were taken from the series of *Lepidodactylus* from Batan Island (n = 14) and all other Philippine/Taiwanese species of the genus (see Specimens Examined). Additional information was taken from Brown & Alcala (1978). Nine meristic and 21 morphometric characters were used for comparisons. The meristic characters are the number of: upper labials (UL), lower labials (LL), internasal scales (INS), interorbital scales (IOS), midbody scale rows (MSR), enlarged preanal and femoral scales (PFS), preanal and femoral pores in males (PFP), toe I scansors (TIS), toe IV scansors (TIVS). The mensural characters are: snout to vent length (SVL), head length (HL), head width (HW), head depth (HD), snout to eye length (SEL), eye diameter (ED), eye to ear length (EEL), internasal distance (IND), interorbital distance (IOD), snout to arm length (SAL), axilla to groin length (AGL), body width (BW), body depth (BD), thigh length (THL), tibia length (TBL), toe I length (TIL), toe IV length (TIVL), toe IV width (TIVW), the length of scansor series beneath toe IV (SL), tail width (TW), and tail depth (TD). All morphometric characters were measured to the nearest 0.1 mm with dial calipers. Meristics were compared using Wilcoxon's 2-sample test and morphometric characters were examined by principal component analysis, using the PRICOMP procedure of SAS (1985) with correlation ma-

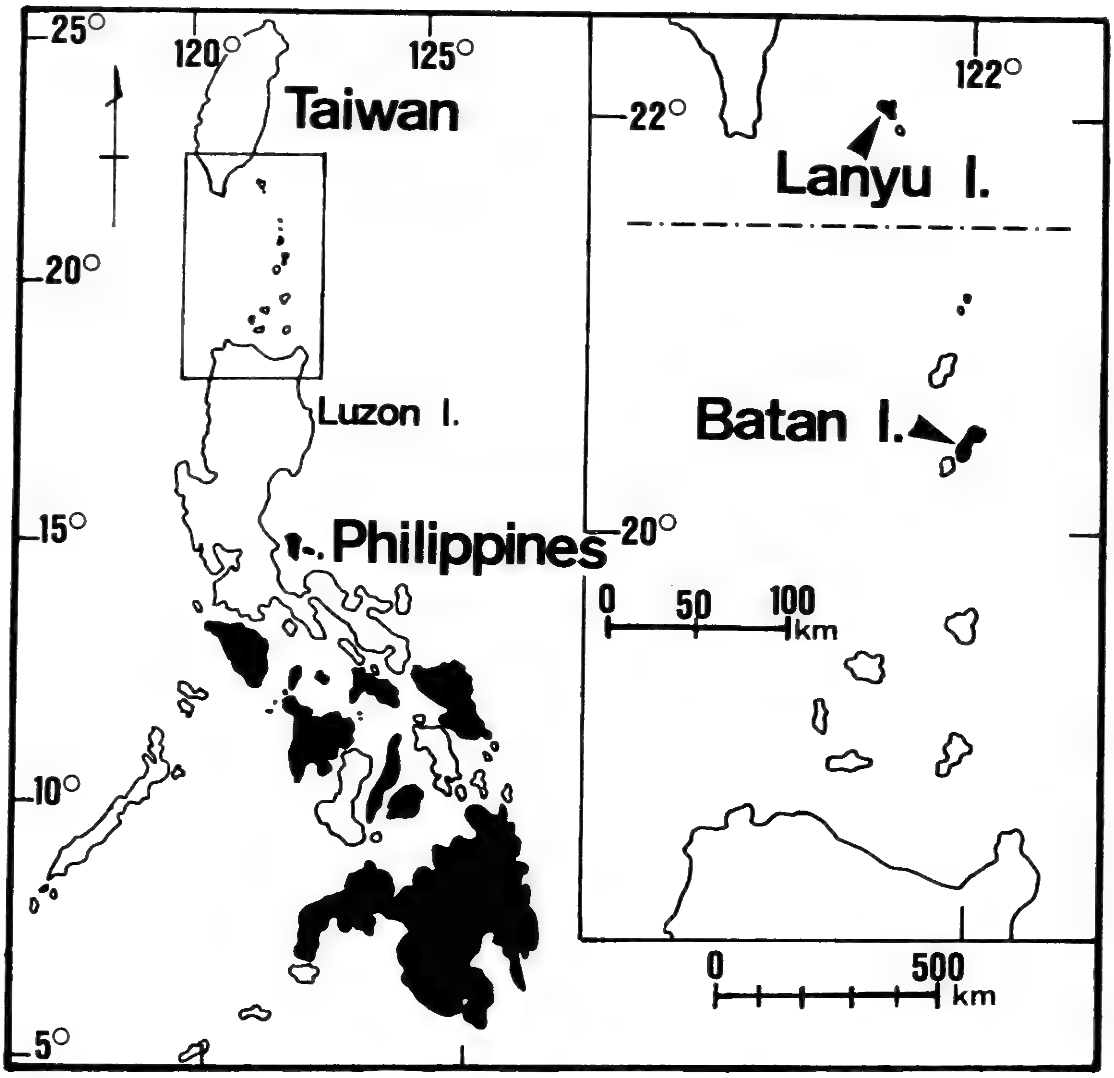

Fig. 1. Map of the Philippines and Taiwan, showing the type locality of *Lepidodactylus balioburius* sp. nov. (Batan Island, inset), in relation to the distribution of its close relative *L. yami* (Lanyu Island, inset) and *L. planicaudus* (shaded portions in the central and the southern Philippines).

trix. Skeletal characters were examined in radiographs. Museum acronyms follow Leviton et al. (1985).

Lepidodactylus balioburius, new species
Fig. 2

Holotype.—Philippine National Museum (PNM) 984 (Original number USNM-FS 121559), an adult male collected 2 km (by road) SE of Mahatao, Mahatao Municipality, Batan Island, Batanes Province, Philippines, on 6 Jun 1985, by Angel C. Alcala, Ven Samarita, and Braulio Gargar.

Paratypes.—(n = 13, all from Batan Island). USNM 266559, 3 km NE of Basco, collected by Charles A. Ross & B. Gargar on 28 May 1985; OMNH 2349 (USNM-FS 121200), 1–2 km E of Basco along road to Balugdh Bay, A. C. Alcala & D. Catada, 27 May 1985; USNM 266560–61, 2.5 km ENE of Basco on W slope of Mt. Iraya, 150 m, Robert S. Kennedy & Fred G. Thompson, 30 May 1985; OMNH 2348 (USNM-FS 121372), Basco, C. A. Ross, 31 May 1985; USNM 266562, 1.5 km N of Basco, near airstrip, C. A. Ross & A. C. Alcala, 4 Jun 1985; USNM 266563, Itbud, C. A. Ross & B. Gargar, 5 Jun 1985; USNM 266564, 3 km ENE of Basco, W slope Mt. Iraya, 150 m, C. A. Ross & R. S. Kennedy, 7 Jun 1985; CAS 162489, Mahatao, A. C. Alcala, 8 Jun 1985; USNM 266565–67, CAS 162490, 2 km E of Mahatao, C. A. Ross & A. C. Alcala,

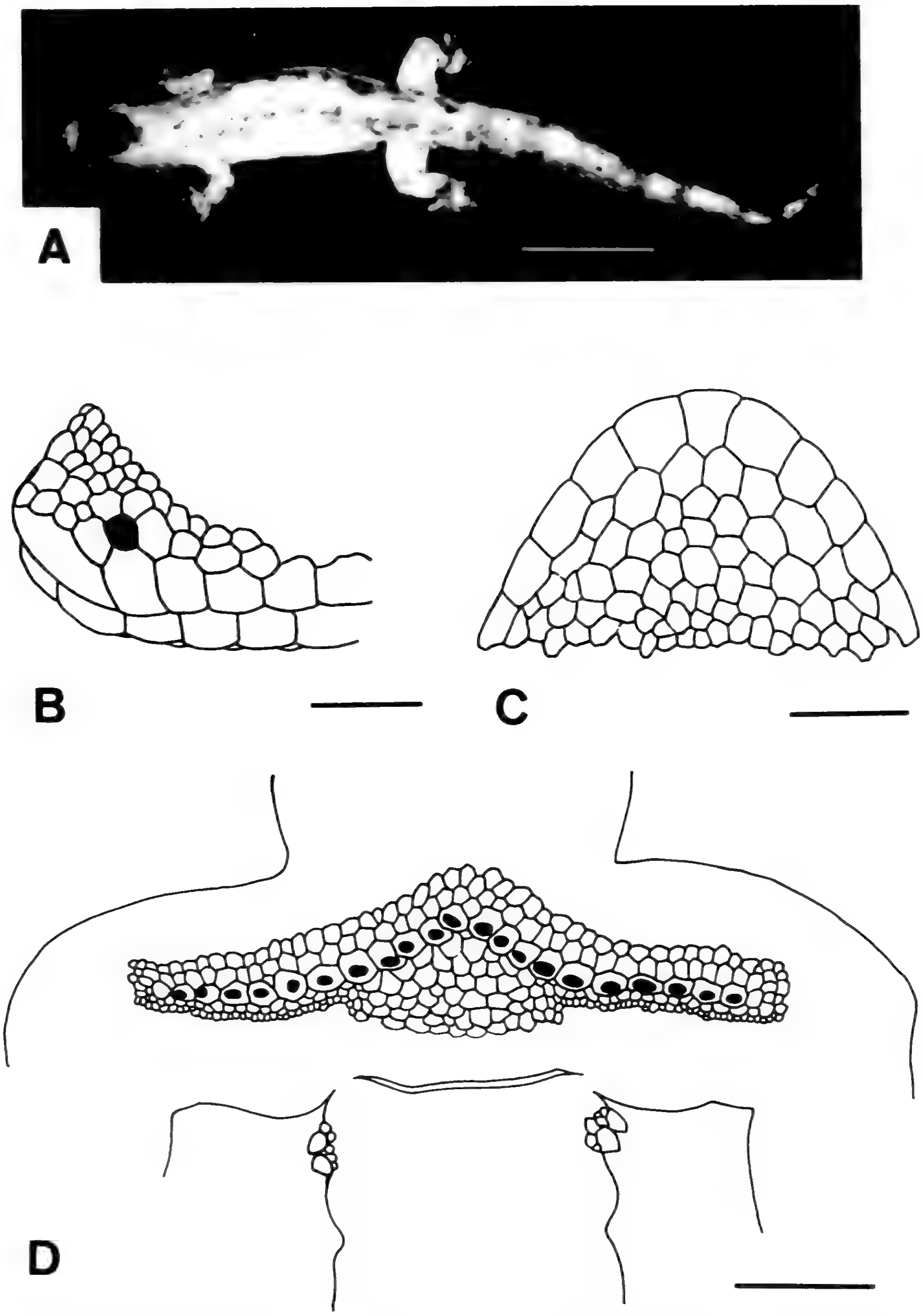

Fig. 2. Holotype (PNM 984) of *Lepidodactylus balioburius,* adult male. A) dorsal view (scale = 10 mm), B) lateral and C) ventral views of snout (scale = 1 mm), D) ventral view of the preanal and femoral region, showing pores and enlarged scales (scale = 2 mm).

6 Jun 1985. (five males and eight females, all adults).

Etymology.—The specific name is derived from the Latin roots balius (brown) and burius (beast), an appropriate descriptor for this species. The name also acknowledges the significant contributions to Philippine herpetology by Walter C. Brown and Charles A. Ross.

Diagnosis.—A small (males 27.2–34.9, females 33.5–38.7 mm), bisexual, Group III (sensu Brown & Parker 1977) species of *Lepidodactylus,* characterized by slight but distinct digital webbing, relatively few enlarged scales and pores in the femoral/preanal region, the rostral separated from the nostril by a scale, presence of lateral serration on the tail, and the absence of distinctive pattern elements (see Figs. 2, 3).

Description of holotype.—Habitus mod-

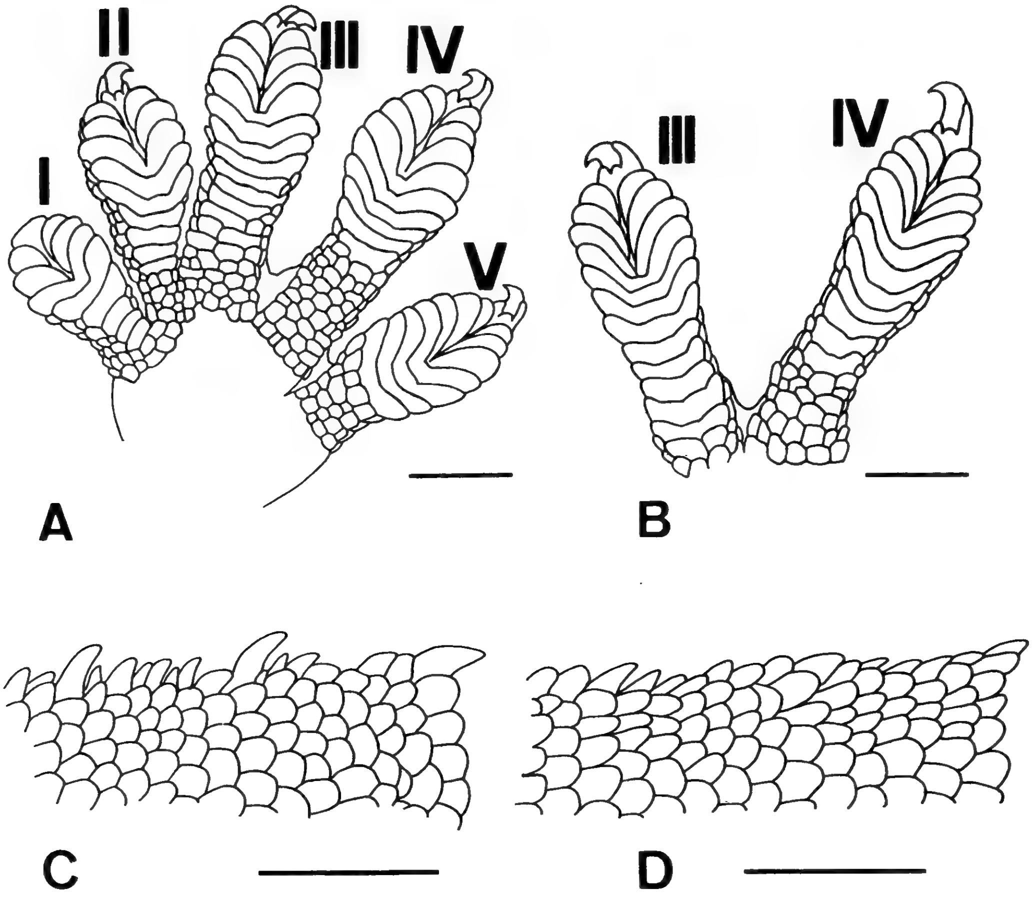

Fig. 3. Ventral view of toes and lateral tail margins of *Lepidodactylus baliobурius* (A & C) and *L. yami* (B & D).

erately depressed, SVL 30.4 mm. Snout tapering, rounded at tip, length 3.9 mm. Eye diameter 2.1 mm. Internasal distance 1.6 mm. Rostral separated from nostril by a small quadrangular scale. Nostril surrounded by two supranasals, first upper labial, one small scale anteriorly and a slightly enlarged scale posteriorly. Anterior supranasals separated by two small scales that border the rostral. Eleven upper labials on the right, 12 on the left, the 9th beneath the center of the orbit; the last 2 only about twice as large as the surrounding scales. Eleven lower labials. Mental triangular, smaller than adjacent labials. Three to 5 rows of slightly enlarged scales on anterior part of chin. Scales on the snout larger than those on the dorsal surface of the body. Dorsal and lateral body scales very small, granular, with no enlarged tubercles. Forty-one interorbital scale rows at the midpoint of orbits, 131 scale rows at midbody. Ventral scales flat, cycloid, distinctly larger than dorsals.

Length of extended hind limb 11.0 mm. Digits moderately dilated, distal three-fifths to three-quarters of undersurface bearing scansors as follows: fingers—I 7, II 8, III 10, IV 11 (right) or 12 (left), V 8; toes—I 8, II 9, III 11 (left) or 12 (right), IV 9 (right) or 10 (left), V 8 (left) or 9 (right). Distal two to three scansors, including the terminal one, divided on all digits except the first. First digit with complete terminal and two divided subterminal scansors. All digits except the first clawed. Compressed claw-bearing phalanges arising from distal margin of the dilated part and extending only a short distance beyond. Phalangeal formula of hand and foot 2-3-4-5-3. Webbing slight but evident between toes III and IV, extending to about one-eighth to one-fifth length of toe IV.

Twenty-three enlarged preanal and femoral scales bearing a continuous series of 21 pores, extending over proximal 60% of thigh. Series of pore-bearing scales followed by one row of slightly enlarged scales on thigh, and four to five rows of enlarged scales in preanal region. Two pairs of cloacal spurs on both sides of vent. Tail unregenerated, moderately depressed; its depth just posterior to the basal swollen area 73% of its width; lateral flange of skin lacking, but enlarged, spine-like scales present every five to seven marginal scales. Scales on the ventral surface of the tail slightly larger than those on dorsal surface. Interclavicle dagger-shaped, without lateral projections. Clavicles perforated. Twenty-six presacral vertebrae. Nasals fused at midline.

Color in alcohol.—Dorsal ground color light grayish tan, with numerous minute dark dots; slightly darker areas on snout and between orbits; a wide, indistinct, dark band from the tip of the snout, through the nostril, eye, along the dorsal margin of the ear, and fading out between the ear and forelimb. Several dark spots on upper and lower labial regions. Indistinct rusty gray markings forming vague dorso-lateral lines. Venter creamy white, with minute blackish dots, much sparser than those on dorsum. Tail with 10 dark gray annular bands.

Variation.—Variation in counts and measurements of the type series is presented in Tables 1 and 2. In the five specimens with regenerated tails the enlarged, spine-like lateral scales are absent.

Coloration in the series is variable. In two specimens, the dorsal ground color is much darker and more rusty than the holotype, with a lighter middorsal region forming a broad longitudinal stripe. The dark dorsolateral markings and annular bands on the tail are indistinct or absent in seven specimens. In two others, however, these markings are more distinct than in the holotype. Four specimens have black spots on the lateral region of the original tail and on the neck.

Natural history.—Specimens were collected in both disturbed and forested habitats from sea level to 150 m on Mt. Iraya. The field notes of C. A. Ross indicate that

Table 1.—Comparison of nine meristic characters in *L. balioburius* sp. nov., *L. yami,* and other Philippine congeners. See the text for abbreviations. Data marked with an * taken from Brown and Alcala (1978:82–101 + table 6), but note that numbers in the text do not always agree with those in the table. In these cases, inclusive values were used.

Species		UL	LL	INS	IOS	MSR	PFS	PFP	TIS	TIVS
L. balioburius	$\bar{x}$	11.57	10.07	4.71	40.00	138.57	22.79	21.33	7.71	10.00
	SD	0.94	0.83	0.47	3.57	5.32	1.37	1.37	0.83	0.68
	range	10–14	9–11	4–5	34–46	131–151	20–25	19–23	6–9	9–11
L. yami	$\bar{x}$	12.07	10.93	4.20	43.27	139.60	22.55	19.63	8.40	11.73
	SD	0.80	0.88	0.68	3.81	7.53	1.51	1.92	0.74	1.28
	range	11–14	10–12	3–5	36–49	126–151	19–24	15–21	7–9	10–15
L. planicaudus	range	10–13*	10–12*	3–5*	34–42*	135–145*	18–26*	18–34*	7–9*	7–12*
L. christiani	range	10–13*	10–12*	4–5*	40–41	165–168	20–28*	20–27*	6–9*	7–9*
L. aureolineatus	range	11–13*	9–13*	3–5*	38–42	120–140*	30–40*	26–40*	9–10*	11–16*
L. herrei	range	10–13*	9–13*	3–5*	24–34*	78–108*	32–40*	28–46*	9–11*	12–17*
L. lugubris	range	10–13*	9–12*	3–5*	32–40*	120–140*	28–35*	21–32*	9–13*	12–18*

Table 2.—Comparison of 21 morphometric characters of *Lepidodactylus balioburius* sp. nov. and *L. yami*, and the factor loadings on the first three principal components. See text for abbreviations.

	L. balioburius			*L. yami*					
Characters	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	PRIN I	PRIN II	PRIN III
SVL	34.08	3.81	27.2–38.7	36.16	2.71	31.7–42.1	0.27	0.08	−0.94
HL	8.69	0.67	7.6–9.6	9.47	0.69	8.6–10.9	0.27	−0.01	−0.03
HW	6.36	0.47	5.6–7.1	6.76	0.95	6.0–9.8	0.25	0.15	0.10
HD	3.59	0.28	3.1–3.9	4.23	1.19	3.4–7.1	0.25	0.04	−0.13
SEL	4.11	0.35	3.5–4.6	4.19	0.28	3.9–4.8	0.25	0.11	0.02
ED	2.20	0.20	2.0–2.6	2.29	0.23	2.0–2.6	0.23	0.02	0.13
EEL	2.83	0.17	2.5–3.0	3.02	0.13	2.8–3.4	0.24	−0.07	0.00
IND	1.63	0.13	1.4–1.8	1.68	0.14	1.5–2.0	0.23	0.08	0.06
IOD	4.16	0.29	3.7–4.7	4.59	0.36	4.0–5.0	0.17	−0.23	−0.11
SAL	12.59	1.30	10.6–14.8	13.44	1.05	11.5–15.1	0.24	0.10	0.15
AGL	16.19	2.13	12.7–19.3	17.81	1.82	14.9–21.5	0.24	0.04	−0.38
BW	8.23	1.25	6.2–9.9	7.04	1.23	5.6–9.4	0.05	0.48	−0.35
BD	4.23	0.86	2.8–5.4	5.25	1.17	4.0–8.6	0.23	0.01	−0.36
THL	4.43	0.60	3.5–5.3	4.80	0.68	3.5–5.8	0.24	0.06	−0.10
TBL	4.38	0.38	3.6–4.8	4.90	0.36	4.3–5.4	0.26	−0.11	−0.09
TIL	1.65	0.21	1.4–2.1	1.95	0.16	1.7–2.2	0.22	−0.19	0.12
TIVL	3.05	0.37	2.4–3.7	3.72	0.34	3.0–4.2	0.22	−0.21	0.29
TIVW	1.17	0.17	1.0–1.6	1.19	0.14	0.9–1.5	0.20	0.00	0.51
SL	2.12	0.36	1.6–2.9	2.70	0.21	2.2–2.9	0.19	−0.29	−0.00
TW	4.51	0.64	2.9–5.6	3.50	0.45	2.7–4.1	0.02	0.53	0.11
TD	2.97	0.32	2.3–3.4	2.82	0.37	2.1–3.6	0.06	0.44	0.34
Eigenvalue							12.34	3.20	1.15
Difference							9.13	2.06	0.23
Proportion							0.59	0.15	0.05
Cum. prop.							0.59	0.74	0.79

the species was commonly found under loose bark on trees during the day, in disturbed areas of fields and gardens, in coastal vegetation, and along a forested stream. Of those found after dark, one was active on the guest house in Basco, and another was on the underside of a banana leaf in forest on Mt. Iraya. Two eggs (USNM 266568), four hatched eggshells (not collected), and an adult were found under bark in a ravine running through a garden area, eventually leading to forest. Other gekkonids collected with *L. balioburius* include *Hemidactylus frenatus, Gehyra mutilata,* and *Gekko porosus.* Since *L. balioburius* is ecologically tolerant and not restricted to forest, it is likely that it will be found on other islands in the Batan group, none of which has been adequately collected to date.

Distribution.—Known only from Batan Island, Batanes Province, Philippines, but expected on other islands in the group (see above).

Remarks.—Brown & Alcala (1978) conveniently separated the Philippine species of *Lepidodactylus* into two species complexes (=Sections), based largely on digital morphology, habitus, and caudal scalation. Section A (consisting of *aureolineatus, herrei* and *lugubris*) was characterized by high scansor counts (11–18, usually more than 12), the scansors covering most of the moderately to broadly dilated digits, slight digital webbing, moderately depressed habitus, and a slightly to moderately flattened tail with lateral denticulation. Section B species (*christiani, planicaudus*) have fewer scansors (7–10, usually less than 10), confined to the distal half of broadly dilated and strongly webbed digits. The body and tail are strongly flattened, the latter with a broad flange of skin.

Ota (1987) placed his new species, *L. yami* from Lanyu Island, Taiwan, in Section A, but with some reservations. He also restressed the importance of the nostril position relative to the rostral (in contact in Section A species, separated by a scale in *christiani* and *yami,* separated or in contact in *planicaudus*). Brown & Alcala (1978:81) dismissed this character as having "little significance at the species level," due to the variation in *planicaudus,* but our data indicate that it may be more useful than Brown & Alcala thought.

Lepidodactylus balioburius shares the nasal-rostral separation character with *L. yami* and the Section B species, but has little else in common with the latter. Consequently, it requires comparison only with Section A species. Within this group, *L. balioburius* has lower PFS, PFP, TIS, and TIVS counts than all species except *L. yami* (see Table 1). *Lepidodactylus aureolineatus* and *herrei* are further distinguished by the presence of bright head stripes beginning on the snout and extending to near the ear. *Lepidodactylus lugubris* is a functionally all-female, parthenogenetic species; the few males reported to date have been sterile (Cuellar & Kluge 1972, Pasteur et al. 1987). In color and pattern, *L. lugubris* is often very pale, almost white, with a variable pattern of dark spots, occasionally resembling those in the much darker *L. balioburius. Lepidodactylus lugubris* is capable of color change, however. When in the dark phase, a more complex, ladder-like pattern becomes obvious, but this pattern is distinctly different from the plain brown, spotted *balioburius.*

Lepidodactylus balioburius and *L. yami* share a number of characters unique in Section A species. Both are small, brown, unspecialized species isolated on small islands far to the north of their Philippine congeners (reports of *L. lugubris* from Taiwan and associated islands are possibly recent introductions [Ota 1986, Cheng 1987]). Besides the similar habitus, coloration, and nostril-rostral separation, UL, MSR, PFS, and PFP showed no statistically significant differences between the two species ($P \geq 0.05$). Although the ranges overlapped somewhat, the means of LL, INS, IOS, TIS, and TIVS were significantly different (Table 1); INS of *L. balioburius* was larger than *yami* ($P \leq 0.05$), whereas LL ($P \leq 0.05$), IOS (0.05), TIS (0.05), and TIVS (0.001) were larger in *L. yami.* Principal component analysis of morphometric characters revealed approximately 80% of the total variation in shape as expressed in the first three components—PRINs I, II and III. Of these, PRIN I was of little use in separating *L. balioburius* from *L. yami.* This component consists wholly of positive variable loadings, and is primarily a size component (Table 2). PRIN II, accounting for about 15% of the total variance, tends to discriminate *L. balioburius* from *L. yami* more strongly. Variable loadings on this component revealed several characters chiefly contributing to the shape. The greatest proportion of the variance on PRIN II was expressed by differences in TW. The BW and TD were also heavily loaded, and followed by SL, IOD, TIVL, TIL and HW in descending order. Outlines of scatter plots of the component scores on PRINs I and II separated *L. balioburius* from *L. yami* without overlap (Fig. 4). The two species can also be distinguished by toe webbing and lateral caudal scalation, although these two characters are more subjective. *Lepidodactylus balioburius* has slightly more extensive webbing than *L. yami* (Fig. 3A, B) and the lateral denticulation of the original tail of *balioburius* consists of strongly enlarged, spine-like scales (Fig. 3C). In *L. yami,* slightly enlarged scales are present along the lateral tail edge, but they are neither projecting nor spinose (Fig. 3D). We originally intended to summarize and discuss the relationships of Philippine-Taiwanese *Lepidodactylus* in this paper. Unfortunately, the unprecedented variation in *L. planicaudus* requires further re-evaluation so we defer our taxonomic summary and key to a later paper.

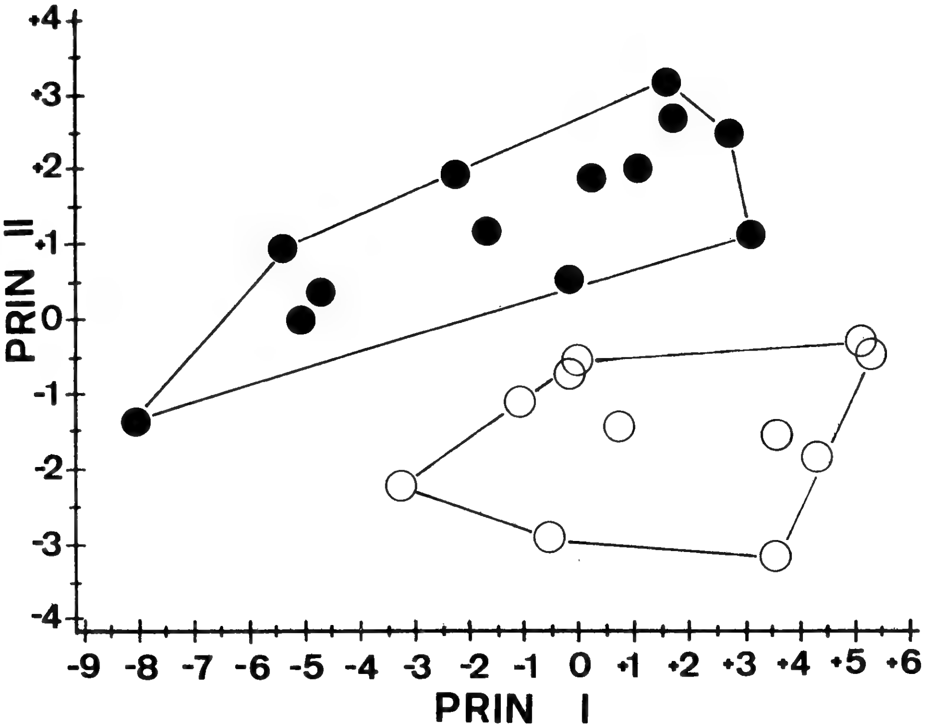

Fig. 4. Two-dimensional plots of scores of *Lepidodactylus balioburius* (closed circles) and *L. yami* (open circles) on principal components (PRINs) I and II. See Table 2 for the factor loadings of each component.

The apparent absence of *Lepidodactylus* from the large island of Luzon is zoogeographically puzzling. Although *L. planicaudus* is found on small islands both east and southwest of Luzon (Brown & Alcala 1978, see also Fig. 1), the genus remains unreported from the entire large island; even the widespread human commensal *L. lugubris* is absent from its towns and cities. Although Luzon has been reasonably well collected (Taylor 1922; Brown & Alcala 1970, 1978), this hiatus may not be real. Many Philippine *Lepidodactylus* are ecologically restricted and difficult to collect. They may inhabit axils of palms or aerial ferns 10 meters or more from the ground. The montane areas of northern Luzon have never been adequately sampled and we would not be surprised if a new species allied to *L. balioburius* and *yami* is eventually discovered in that area.

Specimens examined.—*L. yami:* Osaka Museum of Natural History (OMNH) R2291 (holotype), 690, 691, R2855–61, California Academy of Sciences (CAS) 158254 (paratypes), USNM 267943–44; *L. planicaudus:* CAS 60570, 128566, 139930, 139931, *L. christiani:* CAS 128877, 128878. *L. aureolineatus:* CAS-SU 28411, 26127, CAS 60226, 139941. *L. h. herrei:* CAS-SU 24228, 26342. *L. h. medianus:* CAS 125239, 131856 (paratypes). *L. lugubris:* OMNH R1772, 2201, 2202, 2320, 2321, CAS 158255, 60595, 137835, Australian Museum (AMS) R82602–82610, 82724–82730, 109804–109809, 110141–110146, 110238–110242.

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A NEW SPECIES OF *EUPSOPHUS* (AMPHIBIA: ANURA: LEPTODACTYLIDAE) FROM SOUTHERN CHILE

J. Ramón Formas

Abstract.—*Eupsophus emiliopugini,* a new species of leptodactylid frog, is described from southern Chile. This species is distinguished from its congeners by the olive-green cephalic pigmentation. The mating call is composed of two notes and the tadpole is typically an inhabitant of ground water-filled cavities. This frog occurs from eastern Osorno Province through Llanquihue, Chiloé, and Aisén provinces.

The genus *Eupsophus* Fitzinger, 1843 is restricted to the temperate *Nothofagus* forest of the southwestern border of South America. At present five species have been described (*E. roseus, E. vittatus, E. calcaratus, E. migueli,* and *E. insularis*) (Formas & Vera 1982, Formas 1985), and for this reason *Eupsophus* can be considered the most diverse genus within the reduced anuran fauna of the temperate forest system of southern Chile and Argentina. Among the genera of the sub-family Telmatobiinae, *Eupsophus* is remarkable by having tadpoles (*E. roseus, E. vittatus,* and *E. calcaratus*) which live in small water-filled cavities in the ground. The larval mouthparts (denticles) are reduced, and the larvae feed only upon yolk reserves (Formas & Pugín 1978a, b; Formas 1989).

Between September 1975 and December 1987, Carlos Varela, Lila Brieva, Gonzalo Aguilar and I collected specimens of a new species of *Eupsophus* in the temperate *Nothofagus* forest of southern Chile. In this paper the new taxon is described on the basis of a series of materials (adults, juveniles, mating call, eggs, and tadpoles) collected from seventeen localities.

Eupsophus emiliopugini, new species
Fig. 1

Holotype.—IZUA (Instituto de Zoología, Universidad Austral de Chile) 1587, adult male; Ramón Formas, Nov 28, 1975, at La Picada, 23 km NE (by road) of Ensenada (Fig. 2), Osorno Province, Andean Range, 41°04′S, 72°26′W, 480 m.

Paratypes.—Seven adult males from the type locality: IZUA 1585–86, 1593, 1596, 1602, 1607–8.

Diagnosis.—*Eupsophus emiliopugini* is a medium-sized frog which is characterized by having a distinctive olive-green band between the eyes, which is absent in *E. roseus, E. calcaratus, E. vittatus, E. migueli* and *E. insularis.* Furthermore it differs from *E. vittatus* in snout–vent length (Table 1). The mating call of *E. emiliopugini* has two notes while that of *E. vittatus* possesses five (4–6) notes (Table 2).

Adult description.—(Based on 25 living frogs and 29 fixed specimens.) Head wider than long. Snout pointed in dorsal view, slightly sloping in lateral profile; canthus rostralis indistinct and rounded; loreal region slightly concave; nostrils dorso-lateral, closer to tip of snout than to the orbit; length of the eye greater than distance between eye and nostril; inter-orbital distance narrower than length of eye, greater than internarial distance. Tympanic membranae medium and well defined, tympanum diameter three fourths the distance between eye and nostril. Well developed supratympanic fold extending posteriorly from the corner of the eye to the posterior part of the tympanum, cov-

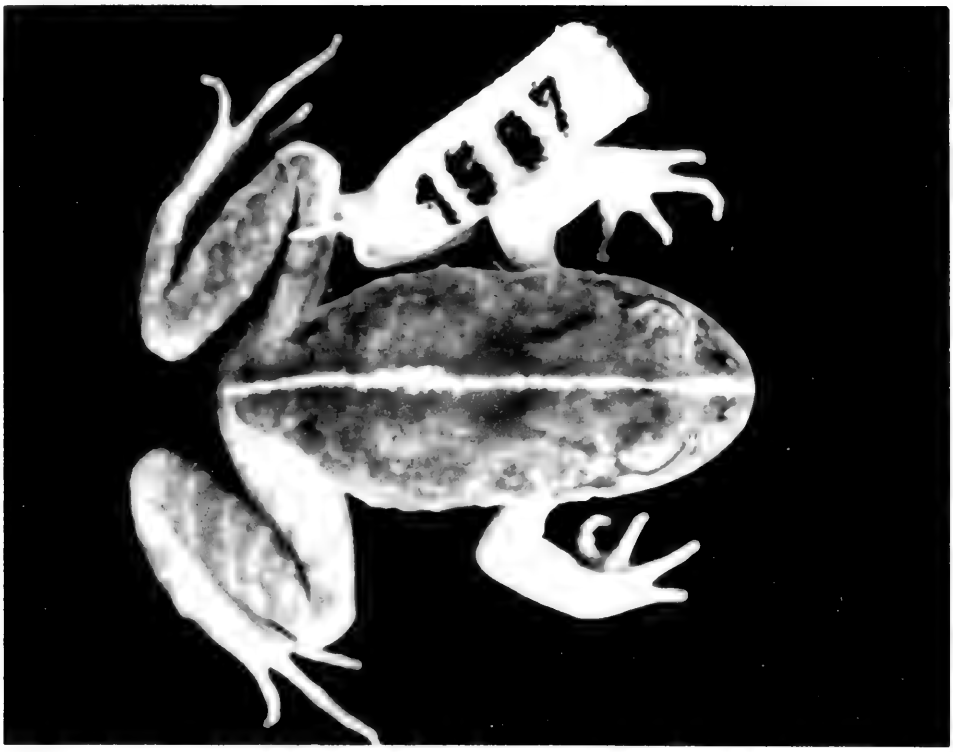


Fig. 1. *Eupsophus emiliopugini*, new species. Holotype (IZUA 1587).

ering upper part of tympanic annulus but not reaching insertion of arm. Tongue large, ovoid, with notch at the tip. Choanae small, round dentigerous process of vomers lying slightly below choanae; each process bearing 3–4 slightly oblique teeth close to median line. Forelimbs thin. First finger equal in length to second; third finger much longer than fourth; digital length in decreasing order 3-4-2-1. Palmar webbing absent; tips of fingers rounded and slightly prominent. Inner median palmar tubercle ovoid; outer palmar tubercle horseshoe-shaped; subarticular tubercles globular and moderate in size; supernumerary palmar tubercles present. Hind limbs slender. Toes long, slender, and moderately fringed; tips of toes rounded; third and fifth toes equal in length; toes in decreasing order of length 4-(3,5)-2-1. Inner metatarsal tubercle ovoid and prominent, outer rudimentary. Subarticular tubercles ovoid; supernumerary tubercles absent. Tarsal fold absent. Rudiment of web among toes. Anal opening oriented transversely and directed postero-ventrally at dorsal level of thighs. Dorsal and ventral skin smooth. Two weakly developed paravertebral folds extending from posterior part of head, converging behind it. Post-tympanic areas and flanks with scarce minute granules. Some specimens with slight granular area around vent and posterior part of thighs. External measurements of males and females of this species shown in Table 1.

Coloration in preservative.—Dorsal ground color light gray with few whitish minute spots; a delicate vertebral line extending from the tip of snout to the vent. A dark greenish band on the eyes. Venter whitish and gular area gray. Lips gray with two or three irregular spots reaching the tympanic region. Arms light gray and crossed by two or three irregular transverse bars of dark gray color in dorsal area; arms and legs whitish ventrally.

Coloration in life.—Dorsal ground color grayish brown to leaden; vertebral line lemon-yellow. Band on eyes olive-green colored. Some specimens with bright yellowish reticulations on the thighs. Belly whitish and the gular area of mature males bright orange.

Distribution.—The presently known range of *E. emiliopugini* extends from northeast-

Table 1.—Comparative measurements (mm) of *Eupsophus emiliopugini* and *E. vittatus.* Means, SD, and ranges (parenthesis).

Character	*E. emiliopugini*		*E. vittatus*	
	Females	Males	Females	Males
n	14	40	19	19
Snout–vent length	50.61 ± 5.01 (41.0–64.0)	46.71 ± 24.00 (42.9–50.0)	59.61 ± 6.38 (47.0–71.8)	55.44 ± 8.68 (44.5–66.6)
Head length	17.93 ± 1.82 (13.4–20.8)	16.45 ± 0.69 (14.8–18.1)	20.43 ± 1.50 (16.7–23.9)	18.36 ± 2.30 (15.4–21.3)
Head width	19.83 ± 2.19 (15.9–25.6)	18.48 ± 0.33 (16.9–19.1)	23.66 ± 2.02 (19.9–26.6)	21.72 ± 3.38 (18.1–26.0)
Femur length	23.38 ± 2.47 (17.1–29.2)	21.96 ± 1.06 (16.6–24.3)	28.45 ± 1.89 (24.7–31.2)	26.37 ± 3.83 (21.7–31.6)
Tibia length	24.2 ± 2.0 (19.9–29.6)	24.25 ± 4.43 (19.30–33.1)	28.98 ± 2.05 (25.0–32.2)	27.2 ± 4.18 (22.8–33.1)
Foot length	35.9 ± 3.56 (29.1–44.9)	36.52 ± 7.10 (29.7–49.1)	41.83 ± 3.56 (34.4–48.2)	41.26 ± 5.37 (33.8–49.1)

ern Osorno Province (Termas de Puyehue) to Aisén Province (Caleta Vidal) (Fig. 2). This area is covered by humid and cool *Nothofagus* forests, which are found at the Andes Cordillera (below 1000 m), the Coastal Range, the Central Valley, and on Chiloé Island. The altitudinal distribution of *E. emiliopugini* ranges between the sea level (Caleta Vidal) and 700 m in the Andes Cordillera (Termas de Puyehue). Over much of its range, *E. emiliopugini* occurs sympatrically with *E. calcaratus.* It has never been found in sympatry with *E. vittatus.*

Habitat.—La Picada (type locality) (Fig. 2) is a small subandean valley surrounded by forests (*Nothofagus, Aextoxicum,* and *Eucryphia*). During winter and summer, frogs were found there under logs, however during the reproductive period (springtime) the animals were collected at the border of a small stream shaded by ferns (*Dryopteris*) and mosses (*Sphagnum* and *Hygroamblystegium*).

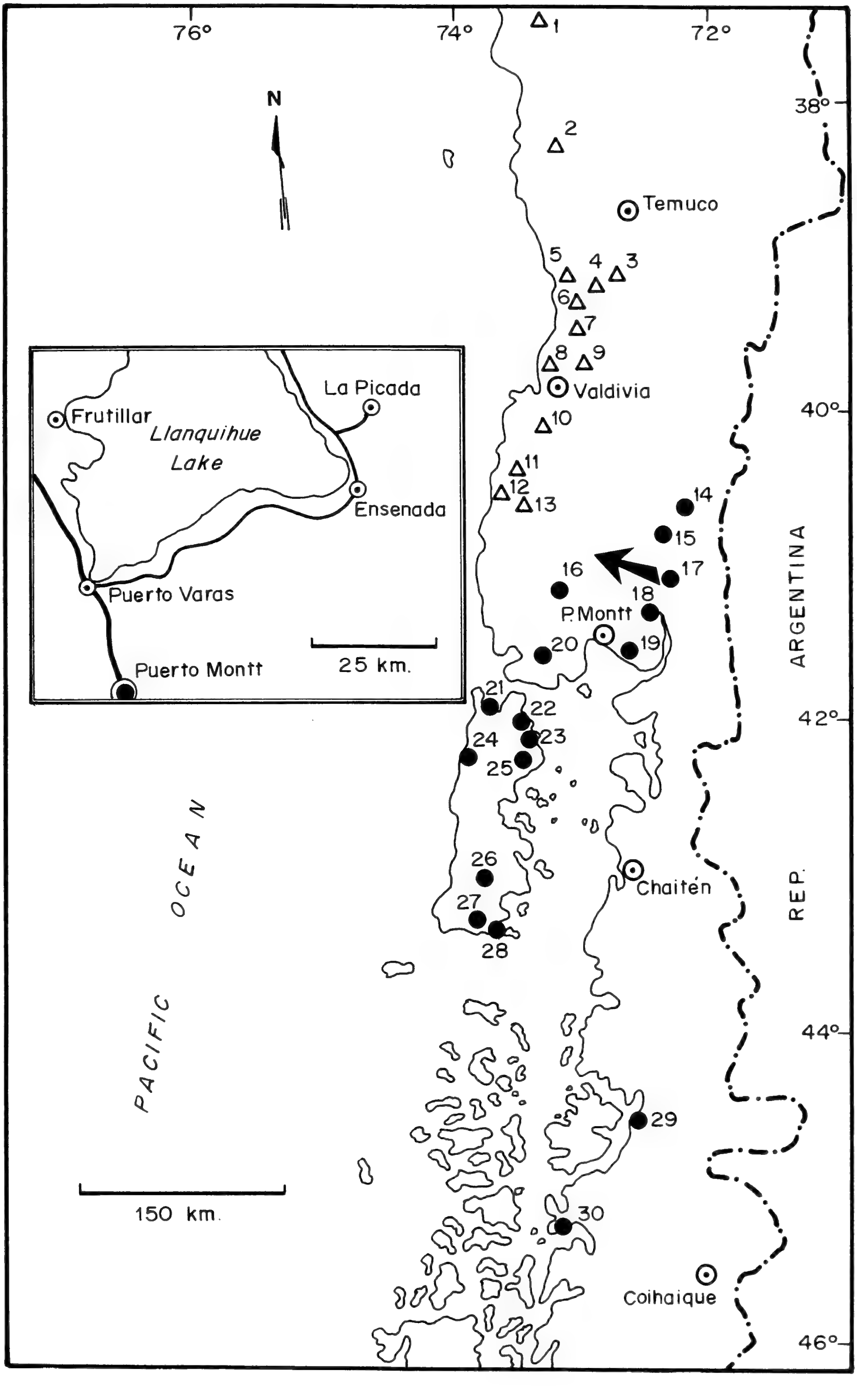
From the ecological point of view this area is situated in the oceanic region of mediterranean influence (di Castri 1968). The annual mean temperature of this region is 10.5°C the relative humidity is 84% and the rainfall ranges between 2000 to 2500 mm. Of seventeen examined localities, fifteen are included in the preceding region; however the southernmost localities (Río Cisnes and Caleta Vidal) are situated in the oceanic cold-temperate region (di Castri 1968). The annual mean temperature is 8.8°C, the relative humidity is 87% and the rainfall ranges from 2500 to 3000 mm.

At the type locality the following species of amphibians were also collected: *Rhinoderma darwinii, Bufo variegatus, Batrachyla leptopus, B. antartandica, Alsodes monticola, Pleurodema thaul, Hylorina sylvatica* and *Eupsophus calcaratus.*

Breeding sites and breeding season.—Ten breeding sites were examined (Termas de Puyehue, La Picada, El Traiguén, Río Rol-

⟶

Fig. 2. Distribution of *Eupsophus emiliopugini* (dots) and *E. vittatus* (triangles) in Southern Chile. Arrow indicates location of the type locality (La Picada) of *E. emiliopugini.* 1) Ramadillas, 2) Contulmo, 3) Máfil, 4) Linguento, 5) Mehuín, 6) San Martín, 7) Los Molinos, 8) Valdivia, 9) Huellelhue, 10) Tres Chiflones, 11) Cordillera Pelada, 12) Bahía Mansa, 13) Pucatrihue, 14) Puyehue, 15) Piedras Negras, 16) El Traiguén, 17) La Picada, 18) Río Rollizo, 19) Río Lenca, 20) Camino Maullín, 21) Ancud, 22) Lechagua, 23) Chepu, 24) Cucao, 25) Puntra, 26) Tepuhueico, 27) Yaldad, 28) Quellón, 29) Río Cisnes, 30) Caleta Vidal.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Puerto Montt
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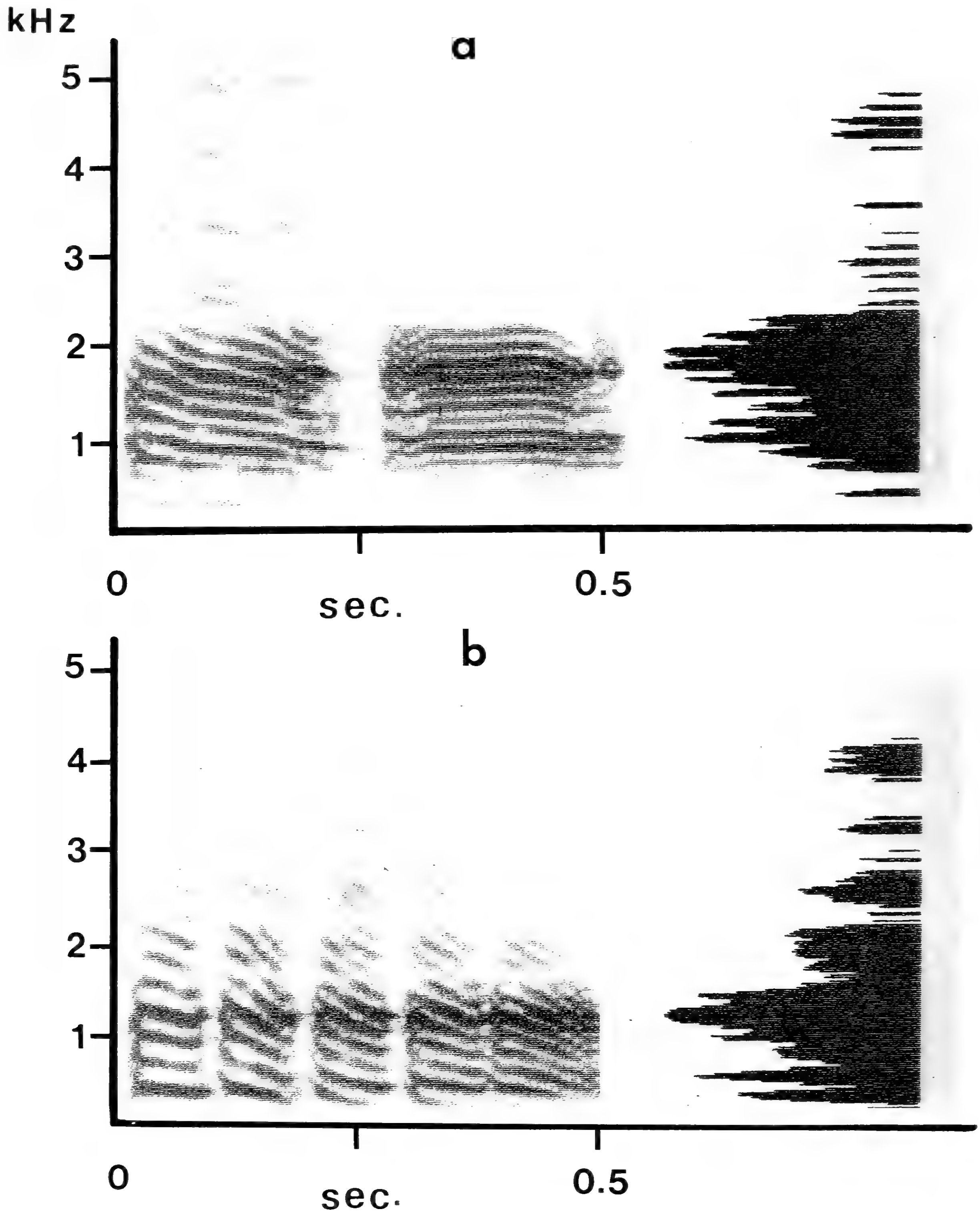

Fig. 3. Audiospectrograms (left) and sections (right) of the mating call of *Eupsophus emiliopugini* (a) and *E. vittatus* (b), band filter 300 Hz.

lizo, Río Lenca, Maullín, Puntra, Cucao, Yaldad, and Caleta Vidal) primarily at La Picada (type locality) and Puntra. Calls have been heard from September to December. Mature females with white oocytes were collected in October (La Picada and Cucao) and tadpoles have been found in December (Puntra). Males with nuptial asperities were collected from September to December. The breeding sites are series of small water-filled cavities at the border of the streams near the forests.

Mating call.—The mating call of *E. emiliopugini* was recorded at seven localities

Table 2.—Characteristics of the mating call of *Eupsophus emiliopugini* and *E. vittatus*. Observed ranges in parenthesis below means; *E. emiliopugini* recorded at Puntra (Chiloé Province) and *E. vittatus* recorded at Mehuín (Valdivia Province). (n = number of analyzed calls.)

Character	*E. emiliopugini*	*E. vittatus*
n	10	10
Notes per call	2	5 (4–6)
Notes duration (sec)	0.203 (0.132–0.250)	0.089 (0.062–0.187)
Pulses per note	25.45 (17–34)	15.90 (11–23)
Dominant frequency (Hz)	1132.08 (500–2000)	1154.34 (600–1680)

(Termas de Puyehue, La Picada, El Traiguén, Río Rollizo, Maullín, Puntra, and Yaldad), and 37 frogs were recorded (5°–16°C). The description of the mating call is based on 10 calls from five animals from Puntra. Males of this species were observed and collected while they were calling from cavities in the ground, at the border of a stream. At this locality males were isolated; however, in the other sites a moderate aggregation was observed. The mating call of *E. emiliopugini* is characteristically composed of two notes (Table 2, Fig. 3). Both are similar in duration ($\bar{x} = 0.20 \pm 0.027$ sec) and have 27 pulses (mean) per note. The fundamental frequency ranges between 85 and 633 Hz and the dominant frequency is spread between 729 and 1320 Hz. Analysis of numerous field recordings demonstrated only minor variations in call characteristics among individuals from different populations. In three localities (La Picada, Río Rollizo, and Puntra) *E. emiliopugini* and *E. calcaratus* were collected calling in close physical association.

Eggs.—A female collected at the type locality (La Picada), 24 Sep 1983, had 148 mature oocytes. At the same place (29 Oct 1984 and 21 Nov 1985) two clutches, containing 166 and 131 eggs (5.78–6.9 mm diameter) respectively, were found in water-filled cavities covered by mosses (*Sphagnum*). Eggs were stuck to one another and were creamy-white in color.

Table 3.—Measurements (mm) ($\bar{x} \pm$ SD) of 30 tadpoles of *Eupsophus emiliopugini* at developmental stage 37 (Gosner 1960).

Total length	23.2 ± 0.74
Body length	9.6 ± 0.24
Body deep	5.0 ± 0.21
Fin deep	6.5 ± 0.36
Snout–nostril distance	1.2 ± 0.002
Interocular distance	1.7
Eye diameter	1.0 ± 0.009
Mouth width	2.5 ± 0.12

Tadpole.—131 larvae of *E. emiliopugini* were collected in a water-filled cavity near (20 cm) a cold stream (12°C) at Puntra (6 Dec 1984). The measurements of the tadpoles are indicated in Table 3. Gosner's (1960) developmental stages are used in the following description. Larvae in stage 37 (Fig. 4a, b) with body ovoid in lateral view, two times longer than deep; contour of the snout flattish. Nostrils small, situated between eye and snout tip. Eyes lateral, diameter 1.7 times the interocular distance. Mouth small and anteromedial, labial papillae interrupted anteriorly, few denticles and tooth formula 2/2; beak well developed. Anal tube medial; no spiracle but small ventrolateral fissure on the left side of the body. Caudal musculature robust, dorsal and ventral fins well developed; end of tail rounded. Color in life creamy-white abdomen and fins transparent; internal organs visible. Minute melanophores among the nearest muscular septa to the body. Dorsal areas of head and trunk scarcely pigmented. On completion of metamorphosis (10 Mar 1985) frogs were 10.1–10.6 mm in snout–vent length. Froglets have the dorsum gray with two well developed paravertebral folds also found in the adults.

Juvenile.—Juveniles (five fixed specimens from La Picada) exhibit the same

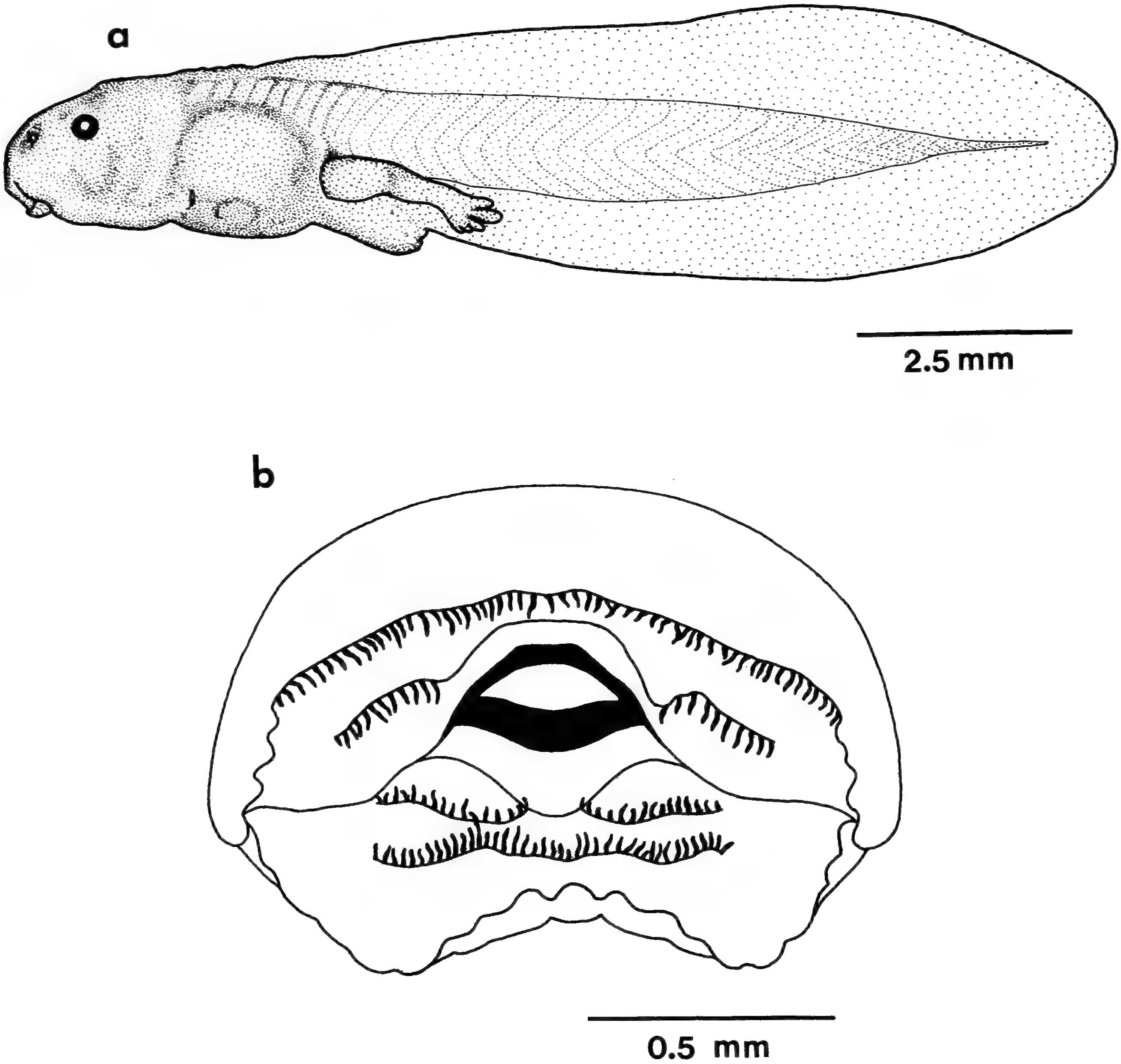

Fig. 4. Tadpole of *Eupsophus emiliopugini,* lateral view (a) and mouth (b). Gosner stage 37.

characteristics of the adults; however, some differences were observed. The two paravertebral folds are well developed and the dorsum and flanks are covered by minute granules. The gular area is dark gray and the olive-green interocular band is not evident.

Variation.—Measurements of 54 adults (40 males and 14 females) (Table 1) show sexual size dimorphism. Of the 99 specimens examined (54 adults and 45 juveniles), 59 specimens (60.2%) have a mid-dorsal line, 38 specimens lack a mid-dorsal line (37.7%) and two specimens (2.1%) from Puntra (IZUA 2060, 2062) exhibit scattered whitish irregular spots on a dark background.

Etymology.—The trivial name honors the memory of my friend and colleague Prof. Dr. Emilio Pugín, for his contribution to knowledge of the reproductive biology and development of the Chilean frogs.

Comparisons

When the adult snout–vent length of *E. emiliopugini* (males $\bar{x}$ = 46.7 mm; females $\bar{x}$ = 50.6 mm) is compared with that of other *Eupsophus* species, it is observed that this frog is as large as *E. vittatus (males* $\bar{x}$ = 54.4 mm; females $\bar{x}$ = 59.6 mm) (Table 1). Both taxa differ from their smaller congeners *E. roseus* (36.6 mm in snout-vent length), *E. migueli* (35.5 mm), *E. calcaratus* (35.1 mm), and *E. insularis* (39.9 mm) (Formas and Vera 1982).

In habitus and dorsal pattern, *E. emiliopugini* is similar to *Eupsophus vittatus*; however, both species differ in external features. *Eupsophus emiliopugini* has an olive-green band between the eyes, which is absent in *E. vittatus.* Furthermore, the latter has the vertebral line wide and creamy-white in color while in *E. emiliopugini* it is narrow and lemon-yellow colored.

Remarkable differences are found between the mating calls of *E. emiliopugini* and *E. roseus, E. migueli,* and *E. calcaratus.* The mating call of *E. emiliopugini* has two notes while the other species presents only one note (Formas 1985). Differences between the voices of *E. emiliopugini* and *E. vittatus* are presented in Table 2 and Fig. 3.

From the geographical point of view *E. emiliopugini* and *E. vittatus* demonstrate a different range of distribution (Fig. 2). Both taxa are allopatric, and *E. vittatus* is distributed in the Coastal Range and the Central Valley between Ramadillas (37°18′S; 73°14′W) and Bahía Mansa (40°33′S; 73°46′W).

Specimens Examined

Abbreviations.—Instituto de Zoología, Universidad Austral de Chile (IZUA); Field Museum of Natural History (FMNH); Museo de Zoología, Universidad de Concepción (MZUC); Juan Carlos Ortíz (personal collection) (J.C.O.); Nelson Díaz (personal collection) (N.D.).

Eupsophus emiliopugini. (99) Osorno: Puyehue (40°42′S; 72°18′W), IZUA 1931, 1933–34, 2012 (tape); Piedras Negras (40°53′S; 72°27′W), IZUA 1951–53; La Picada (41°04′S; 72°26′W), FMNH 218584–85, IZUA 1585–88, 1950, 1953, 1608, 1955–75, 2101 (tape). Llanquihue: Río Lenca (41°37′S; 72°40′W), IZUA 1939, 1948–50, 1939–45; El Traiguén (41°11′S; 73°25′W), IZUA 2103 (tape); Río Rollizo (41°27′S; 72°20′W), IZUA 2104 (tape); Road to Maullín (41°41′S; 73°21′W), IZUA 2102 (tape). Chiloé: Ancud (41°52′S; 73°50′W), J.C.O. 61/1–61/3, 68/13, 33/3; Lechagua (41°53′S; 73°51′W), FMNH 154829–30; Chepu (42°03′S; 74°02′W), MZUC 11939; Puntra (42°07′S; 73°49′W), IZUA 2059–64, 2104 (tape); Tepuhueico (42°47′S; 73°58′W), (2 adults and 6 juveniles untagged); Cucao (42°37′S; 74°07′W), IZUA 1627–28; Quellón (43°07′S; 73°37′W), FMNH 3715; Yaldad (43°07′S; 73°43′W) 2078–95, 2105 (tape). Aisén: Puerto Cisnes (43°30′S; 71°19′W), FMNH 132050–52, 132317, 132659; Caleta Vidal (45°16′S; 73°27′W), (1 adult untagged).

Eupsophus vittatus. (103) Arauco: Ramadillas (37°18′S; 73°16′W), MZUC 11482; Contulmo (38°S; 73°13′W), IZUA 272/80. Valdivia: Mehuín (39°26′S; 73°10′W), IZUA 832–36, 1644–46, N.D. 1–6, IZUA 2096; San Martín (39°33′S; 72°59′W), IZUA 1716–20, 1724, 2097 (tape), 2028–52; Linguento (39°33′S; 72°59′W), IZUA 1937–38, 2098 (tape); Máfil (39°39′S; 72°57′W), FMNH 3825–27; Ciudad de Valdivia (39°48′S; 73°14′W), IZUA 225–28; Huellelhue (39°44′S; 73°06′W), IZUA 1929–30, 2099 (tape); Los Molinos (39°46′S; 73°18′W), IZUA 1936; Tres Chiflones (40°03′S; 73°10′W), IZUA 2009–27; Cordillera Pelada (40°03′S; 73°10′W), IZUA 1935. Osorno: Pucatrihue (40°26′S; 73°47′W), MZUC 12402, IZUA 1988–2008, 2100 (tape); Bahía Mansa (40°33′S; 73°46′W), J.C.O. 69/74.

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A REDESCRIPTION OF *PSEUDORHOMBUS MEGALOPS*, WITH COMMENTS ON *CEPHALOPSETTA VENTROCELLATA* (OSTEICHTHYES: PLEURONECTIFORMES: PARALICHTHYIDAE)

Dannie A. Hensley and Kunio Amaoka

Abstract.—*Pseudorhombus megalops* has not been recorded in the literature since first described by Fowler (1934) from the Philippine Islands. The species is redescribed from the type specimens and additional material from the Philippine Islands, eastern Indian Ocean, Bali Strait, and Arafura Sea. *Pseudorhombus megalops* has a very distinct black spot or ocellus on the left pelvic fin. The only other Indo-Pacific paralichthyid with a similar character is *Cephalopsetta ventrocellata.* These species are compared and characters are given for their separation. *Cephalopsetta ventrocellata,* previously known from the east and west coasts of India and Pakistan, is shown to range to the Andaman Sea and Gulf of Oman. *Cephalopsetta* has been considered a close relative of *Ancylopsetta* (western Atlantic and eastern Pacific) and *Gastropsetta* (western Atlantic) because they share an elongate left pelvic fin. Osteological characters of the caudal fin, however, support placement of *Cephalopsetta* in with the Indo-Pacific genera *Pseudorhombus* and *Tarphops.*

Fowler (1934) described many new flatfish species collected mainly from the Philippine Islands and adjacent regions. Most authors have overlooked Fowler's publication, apparently because it appeared during the same year as, and thus was not cited in, Norman's (1934) monograph on flatfishes. Most of Fowler's descriptions and figures of the new flatfishes were inadequate. In addition, he based many of his interpretations upon the older classification of Weber & de Beaufort (1929). Thus, the status of most of Fowler's (1934) genera and species was uncertain. One species described in this work was *Pseudorhombus megalops.* The description and figure of this species were poor, and there have been no other published records of *P. megalops.* Additional specimens were recently collected from the eastern Indian Ocean, Bali Strait, and Arafura Sea during the Joint Eastern Tropical Indian Ocean Fishery Survey (JETINDOFISH; see Gloerfelt-Tarp & Kailola 1984). We originally could not identify the JETINDOFISH specimens to species and left them as "*Pseudorhombus* sp. 1" in Gloerfelt-Tarp & Kailola (1984), stating that the species appeared very close to *P. megalops.* Since that time we have found additional specimens from the Philippine Islands and have had the opportunity to make the necessary comparisons with Fowler's types for a positive identification as *P. megalops.*

Dutt & Rao (1965) described *Cephalopsetta ventrocellata* from the east coast of India. The only other published records of the species are those of Kotthaus (1977) from the west coast of India and Pakistan. We have examined additional material from the Andaman Sea, west coast of India, and Gulf of Oman. *Cephalopsetta ventrocellata* shows some similarity to *P. megalops* and can be confused with that species.

In this paper we redescribe *P. megalops*

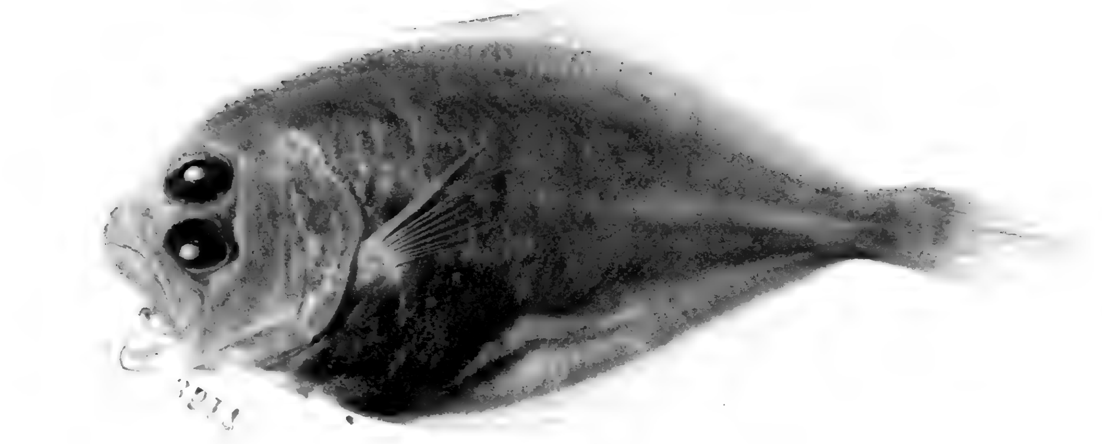

Fig. 1. *Pseudorhombus megalops,* holotype, USNM 93082, 152.0 mm SL.

from the type specimens and additional material and discuss some of the characters and possible phylogenetic position of *C. ventrocellata* and compare it with *P. megalops.*

Materials and Methods

Methods of counts and measurements follow those of Hubbs & Lagler (1949) with two changes. Because all dorsal- and anal-fin rays are unbranched, all ray elements are counted as individual rays. Length of the pelvic fin is the length of the longest ray of that fin. Measurements were made with dial calipers to the nearest 0.1 mm. For regression analysis all variates were transformed to natural logarithms. Standard length was treated as the independent variable. Tests for allometry were performed with the geometric-mean-functional-regression model of Ricker (1973). In this model 95% confidence limits are determined for the slope (v). If unity is outside of these limits allometry is assumed (positive if below, negative if above); isometry is assumed if unity is within the limits.

Caudal-fin drawings were made from radiographs or specimens cleared and stained according to the method of Taylor (1967).

The institutional abbreviations are as follows: ANSP—Academy of Natural Sciences, Philadelphia; CSIRO—Commonwealth Science and Industrial Research Organization, Hobart, Tasmania; FDNR—Florida Department of Natural Resources, St. Petersburg, Florida; HUMZ—Hokkaido University, Laboratory of Marine Zoology, Faculty of Fisheries, Hakodate; NTM—Northern Territory Museum of Arts and Sciences, Darwin, Australia; UPRM—University of Puerto Rico-Mayagüez; and USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C. Standard length and total length are abbreviated SL and TL.

Pseudorhombus megalops Fowler
Figs. 1, 2A–B, 3A–B, 5B, Tables 1–2

Pseudorhombus megalops Fowler, 1934:329, fig. 83 (Philippine Islands).

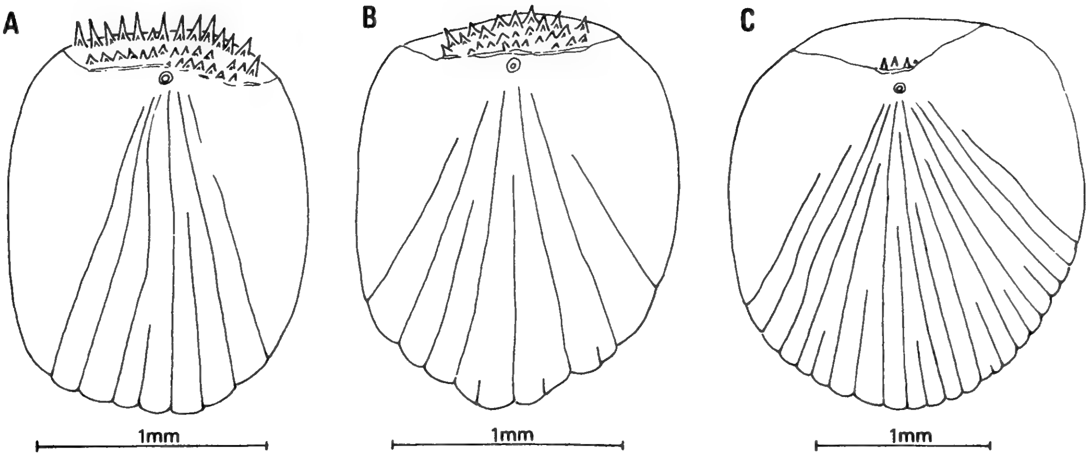

Fig. 2. Scales from near mid-length of body immediately above lateral line: A, left side of *Pseudorhombus megalops,* HUMZ 111769, 146.5 mm SL; B, right side of *P. megalops,* HUMZ 111769, 146.5 mm SL; C, left side of *Cephalopsetta ventrocellata,* ANSP 153379, 161.7 mm SL.

Pseudorhombus sp. 1.—Gloerfelt-Tarp & Kailola, 1984:272 (unnumbered plate), 273, 357 (eastern Indian Ocean, Bali Strait, and Arafura Sea).

Diagnosis.—Dorsal-fin rays 67–70; anal-fin rays 50–53; lateral-line scales 70–77. Gill rakers elongate, 15–18 on lower limb. Lower jaw with 12–20 teeth on blind side, 2–4 large canines near symphysis. Scales on ocular side ctenoid, most scales on blind side ctenoid (Fig. 2A–B). Tip of first interhemal spine stout, usually projecting through body wall anterior to first anal-fin ray. Pelvic fin of ocular side with distinct black spot over fourth or fifth ray (Fig. 3A–B); pelvic fin of blind side longer than that of ocular side.

Description.—Morphometrics as % SL are presented in Table 1. Dorsal-fin rays 67–70; anal-fin rays 50–53; pectoral-fin rays ocular side 11–13, blind side 11–12; pelvic-fin rays ocular side 6, blind side 6; lateral line scales 70–77; gill rakers ocular side 5–9 + 15–18; teeth on blind side of lower jaw 12–20.

Head length 3.0–3.3, body depth 1.9–2.4, both in SL. Measurements in head length are as follows: Snout length 3.9–4.5; upper-jaw length ocular side 2.0–2.2; lower-jaw length ocular side 1.6–1.8; lower-eye length 3.4–4.8; pectoral-fin length ocular side 1.5–1.9, blind side 2.1–2.9; pelvic-fin length ocular side 3.0–4.2, blind side 2.7–3.8; length of first dorsal-fin ray 2.6–3.5, second 3.1–4.0, third 3.6–4.7, fourth 3.6–5.4; length of caudal peduncle 3.6–5.2, depth of caudal peduncle 2.8–3.4.

Anterior profile of head with indentation anterior to upper eye. Anterior margins of eyes at same transverse levels. Posterior end of maxilla below middle to posterior one-third of lower eye. Nostrils of ocular side at same horizontal level as upper margin of lower eye. First dorsal-fin ray variable in position, above either nostril or interspace between nostrils. Tip of isthmus below posterior one-quarter or posterior margin of lower eye. Teeth of upper jaw similar on ocular and blind sides, small and closely spaced laterally with from four to six widely spaced, large canines anteriorly; teeth of lower jaw similar on ocular and blind sides, large and widely spaced laterally with from two to four (usually two) very large canines anteriorly. Lower jaw with prominent symphysial knob. Gill rakers elongate, pointed, with small teeth.

Scales on ocular side ctenoid; most scales on blind side ctenoid, cycloid scales probably being replacement scales (Fig. 2A–B). Supratemporal branch of lateral line reaching one-half to three-quarters of distance to dorsal fin base.

First interhemal spine stout, usually projecting through body wall immediately anterior to first anal-fin ray.

First few dorsal-fin rays slightly elongate.

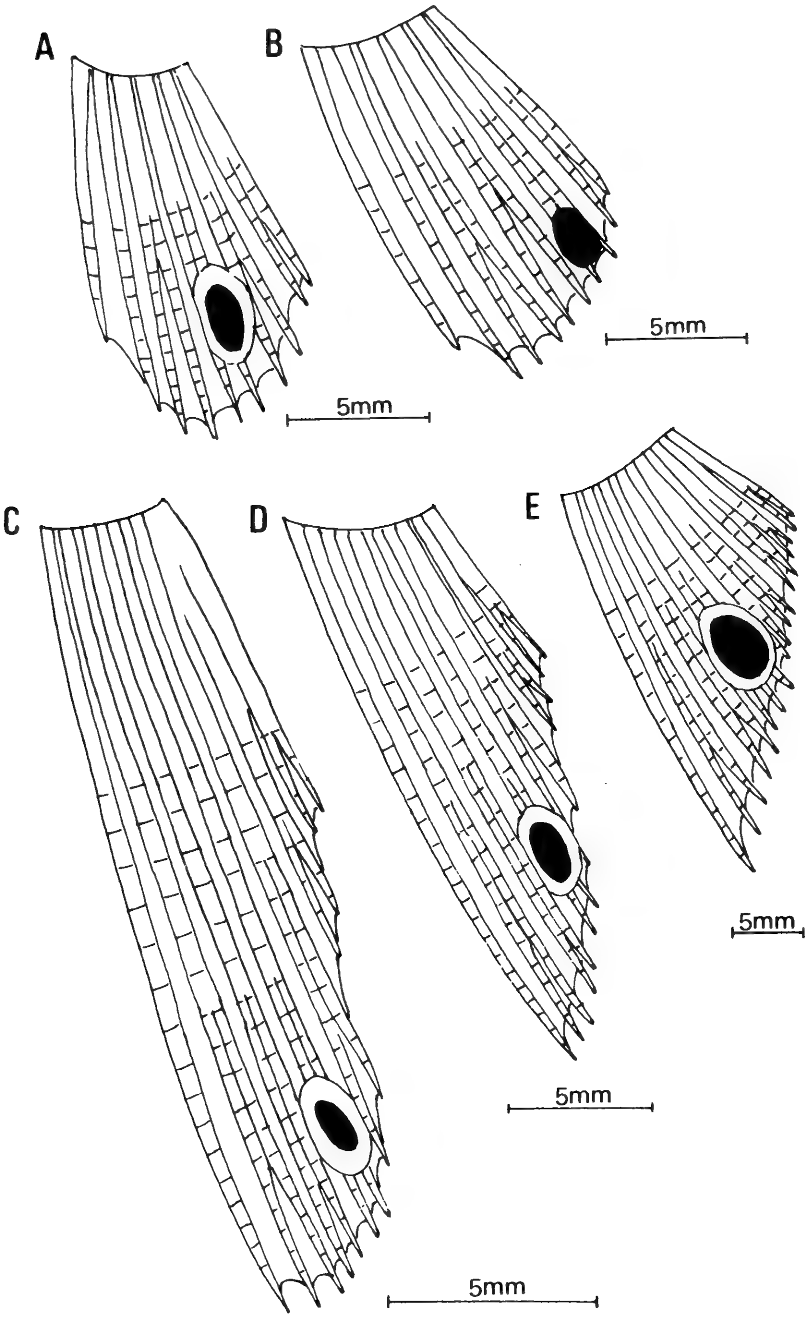

Fig. 3. Left pelvic fins: A, *Pseudorhombus megalops,* CSIRO CA2526, 129.8 mm SL; B, *P. megalops,* holotype, USNM 93082, 152.0 mm SL; C, *Cephalopsetta ventrocellata,* ANSP 153383, 66.0 mm SL; D, *C. ventrocellata,* ANSP 153382, 102.4 mm SL; E, *C. ventrocellata,* ANSP 153379, 161.7 mm SL.

Pelvic fin of blind side slightly longer than that of ocular side.

Color in alcohol.—Ocular side tan to dark grey. Some specimens with dark rings arranged in two longitudinal series above and below lateral line, scattered, smaller dark rings and blotches, and dark streaks on dorsal and anal fins (see unnumbered plate of "*Pseudorhombus* sp. 1" in Gloerfelt-Tarp & Kailola 1984:272). All preserved specimens with distinct black spot on fourth or fifth ray of pelvic fin of ocular side (Fig. 3A–B); some indication that black spot may have white margin in life. Blind side tan or whitish.

Discussion

Norman (1934) recognized 21 species of *Pseudorhombus* Bleeker as valid and three as being of doubtful validity. Subsequently, Fowler (1934) described *P. megalops* and

Table 1.—Morphometric proportions expressed as percentage of SL for specimens of *Pseudorhombus megalops.*

	Holotype (USNM 93082)	Philippine Islands, including paratypes (USNM 93550) (n = 7)	Eastern Indian Ocean, Bali Strait, and Arafura Sea (n = 5)
Standard length (mm)	152.0	131.7–174.7	116.8–154.2
Head length	31.3	31.9–33.4	30.2–33.1
Body depth	48.9	47.4–51.9	40.9–48.4
Upper-jaw length (ocular side)	15.3	15.0–16.1	13.9–16.6
Lower-jaw length (ocular side)	18.9	18.4–19.5	17.6–20.1
Eye length (lower)	8.6	7.9–8.9	6.2–9.2
Snout length	7.2	7.4–8.4	6.7–7.7
Depth of caudal peduncle	9.5	9.5–10.1	9.6–11.0
Length of caudal peduncle	6.8	6.4–7.2	5.8–8.7
Pectoral-fin length (ocular side)	19.3	17.9–22.0	15.8–20.8
Pectoral-fin length (blind side)	14.6	13.0–15.8	10.4–14.5
Pelvic-fin length (ocular side)	8.8	8.0–9.3	7.5–10.9
Pelvic-fin length (blind side)	11.4	8.6–10.5	8.1–11.5
First dorsal-fin ray length	9.9	10.0–11.6	8.7–12.7
Second dorsal-fin ray length	8.5	7.9–9.1	7.6–10.8
Third dorsal-fin ray length	7.8	7.0–8.7	6.5–9.2
Fourth dorsal-fin ray length	7.0	6.1–8.1	7.0–9.2

Amaoka (1969) *P. oculocirris.* Characters given in the "Diagnosis" will distinguish *P. megalops* from all known species of *Pseudorhombus.*

Dutt & Rao (1965) described a new genus and species of paralichthyid, *Cephalopsetta ventrocellata,* from the east coast of India (Visakhapatnam). This species resembles *P. megalops* in having a very distinct black spot enclosed by a light-colored ring between the third and fifth ray of the pelvic fin of the ocular side (Figs. 3, 4). These species are the only known Indo-Pacific paralichthyids with a distinctive dark spot or ocellus on this fin. The South African species *Pseudorhombus natalensis* Gilchrist has a small dark spot on this fin but the spot is relatively diffuse and frequently absent, at least in preserved specimens. Other paralichthyids with an ocellus or distinctive dark spot on the pelvic fin of the ocular side are western Atlantic (*Ancylopsetta kumperae* Tyler, *Paralichthys oblongus* [Mitchill], *Paralichthys isosceles* Jordan) or eastern Pacific species (*Lioglossina tetrophthalmus* Gilbert). *C. ventrocellata* and *P. megalops* can be distinguished by characters presented in Table 2.

Kotthaus (1977) examined specimens of *C. ventrocellata* from the west coast of India and Pakistan and described some additional characters not mentioned by Dutt & Rao (1965). We have examined specimens from the Andaman Sea, eastern Arabian Sea, and Gulf of Oman. Our specimens agree with the descriptions of Dutt & Rao (1965) and Kotthaus (1977) with some exceptions. Dutt & Rao (1965) state that the ocular side has "a few irregular dark blotches." Most of our specimens show distinct dark spots arranged in about five longitudinal rows. The most distinctive dark spots are those immediately below the bases of the dorsal and anal fins and usually a series of three spots along the lateral line. In some specimens there is a faint pattern of several broad, dark transverse bars. Kotthaus (1977) describes the dorsal-fin origin as being immediately above the posterior nostril on the blind side. This character is variable in our specimens, the base of the first dorsal-fin ray being above either nostril or the space between them. According to Dutt & Rao (1965), *C. ventrocellata* has scales with very weak ctenii on the ocular side of the body and cycloid scales on the head and blind side. Kotthaus

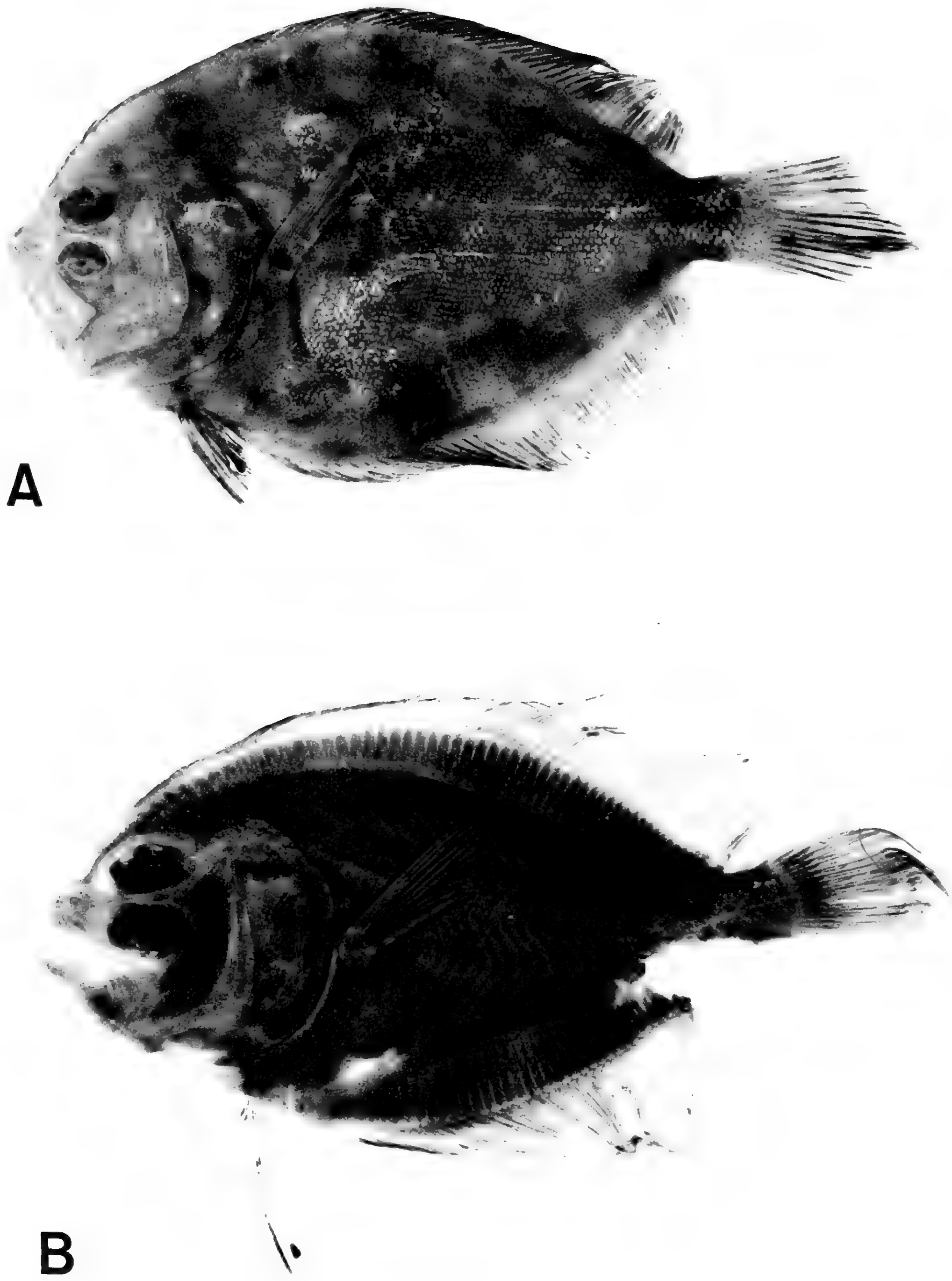

Fig. 4. *Cephalopsetta ventrocellata*: A, adult, ANSP 153379, 168.4 mm SL; B, juvenile, ANSP 153383, 66.0 mm SL.

(1977) expanded on this by saying the scales are covered by skin. Scales on the ocular side of our specimens are covered by skin with only their posterior edges visible. They appear to be cycloid except for some very small ctenii proximal to the exposed edges (Fig. 2C). The specimens we examined have the elongate left pelvic fin described by Dutt

Table 2.—Characters useful for distinguishing *Pseudorhombus megalops* and *Cephalopsetta ventrocellatus*.

	P. megalops	*C. ventrocellatus*
Standard length/head length	3.0–3.3	2.3–3.1 (usually 2.3–2.9)
Head length/length of pelvic fin of ocular side	3.0–4.2	1.4–2.3
Head length/snout length	3.9–4.5	4.7–5.9
Length of pelvic fin of ocular side/length of pelvic fin of blind side	0.8–0.9	1.2–1.8
Number of teeth on lower jaw on blind side	12–20	23–31
Morphology of lower-jaw teeth	Widely spaced, large canines anteriorly	Closely spaced, no large canines
Scales on ocular side	Well-developed ctenii	Feeble ctenii
Scales on blind side	Most ctenoid	Cycloid

& Rao (1965) and Kotthaus (1977). In addition, our specimens showed negative allometric growth of this fin (v = 0.5492 ± 0.1437). Thus, our smallest specimen (66.0 mm SL) had a left-pelvic-fin length of 28.9% SL, specimens of 100.7–168.4 mm SL 16.8–22.2% SL, and a 207.5-mm-SL specimen 15.6% SL (Figs. 3C–E, 4).

The major characters used by Dutt & Rao (1965) to define *Cephalopsetta* are a large head (2.3–3.1 in SL) and an elongate left pelvic fin. *Ancylopsetta* Gill (western Atlantic and eastern Pacific) and *Gastropsetta* Bean (western Atlantic) also have the pelvic fin of the ocular side longer than that of the blind side, and were thus treated by Norman (1934) as being closely related and distinct from other paralichthyid genera. For the same reason Dutt and Rao considered *Cephalopsetta* closely related to *Ancylopsetta* and *Gastropsetta* and restricted their comparative statements to these genera.

Current knowledge of relationships within the Paralichthyidae was recently reviewed by Ahlstrom et al. (1984) and Hensley & Ahlstrom (1984). These authors regard *Cephalopsetta* as a member of the *Pseudorhombus* group (along with the Indo-Pacific genera *Pseudorhombus* and *Tarphops* Jordan & Thompson), a group they considered as probably monophyletic. *Ancylopsetta* and *Gastropsetta* were left in a group (referred to as the *Paralichthys* group) composed of *Paralichthys* Girard, *Hippoglossina* Steindachner, *Lioglossina* Gilbert, *Verecundum* Jordan, and *Xystreurys* Jordan & Gilbert; the authors could find no current evidence for monophyly of this group.

Much of the evidence Ahlstrom et al. (1984) and Hensley & Ahlstrom (1984) used for placing *Cephalopsetta* in the *Pseudorhombus* group and excluding *Ancylopsetta* and *Gastropsetta* involved caudal-fin structure. Species of the *Paralichthys* group have 18 caudal-fin rays, at least one free epural (except in one species of *Hippoglossina* [Sumida et al. 1979]), and a splinter ray on the base of the ventralmost caudal-fin ray (Fig. 5C). The splinter ray is probably a remnant of a ray lost through fusion with an adjacent ray (Okiyama 1974). Amaoka (1969) and Hensley & Ahlstrom (1984) considered these characters as probably being plesiomorphic. The *Pseudorhombus* group usually has 17 caudal-fin rays, the epural fused to the fifth hypural and no splinter ray (Fig. 5A–B). These authors regarded these characters as probably derived and indicative of monophyly.

Although we tentatively treat *Cephalopsetta* as a member of the *Pseudorhombus* group, it should be noted that Gutherz (1966) found that juveniles of *Ancylopsetta antillarum* Gutherz and *Gastropsetta frontalis* Bean have greater relative lengths of left pelvic fins than adults, a growth pattern similar to that seen in *C. ventrocellata*. However, other paralichthyids are known to have elongate left pelvic fins at some stage of development. Several species of what

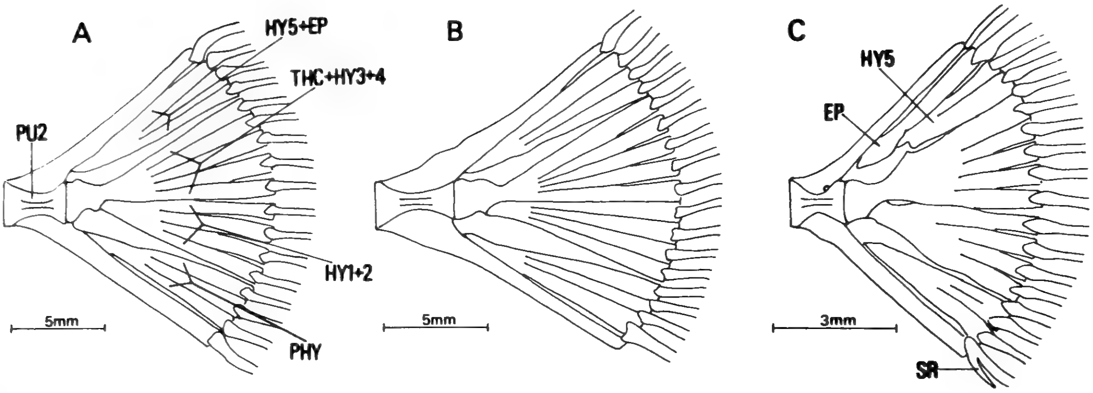

Fig. 5. Caudal skeletons: A, *Cephalopsetta ventrocellata,* ANSP 153379, 161.7 mm SL; B, *Pseudorhombus megalops,* HUMZ 111769, 146.5 mm SL; C, *Ancylopsetta quadrocellata,* FDNR 6115, 52.9 mm SL; abbreviations: EP = epural; HY 1–5 = hypurals 1–5; PHY = parhypural; PU2 = preural centrum 2; SR = splinter ray; THC = terminal half-centrum.

Ahlstrom et al. (1984) and Hensley & Ahlstrom (1984) called the *Cyclopsetta* group have elongate pelvic fin rays on the ocular side as larvae, while adults have short pelvic fins of approximately equal length (see Ahlstrom et al. 1984). Nielsen (1963) has shown that post-metamorphic individuals of at least one species of *Cyclopsetta* (named *Dorsopsetta norma* in Nielsen 1963) have elongate rays in the left pelvic fin. A more detailed comparative analysis of pelvic-fin growth patterns is needed before they can be used for phylogenetic inference.

Material examined.—Pseudorhombus megalops: Philippine Islands: USNM 93082, holotype, 152.0 mm SL; USNM 93550, paratypes, 2 specimens, 141.1–147.8; USNM 93551, 2, 131.8–136.4; USNM 93548, 2, 144.3–174.7; USNM 93549, 131.7. Indian Ocean (south coasts of Sumatra, Java, and Lombok): HUMZ 111768, 154.0; HUMZ 111769, 146.5; NTM 10760-006, 154.2. Bali Strait: NTM S.11022-002, 116.8. Arafura Sea: CSIRO CA2526, 129.8.

Cephalopsetta ventrocellata: Gulf of Oman: ANSP 153383, 66.0. India (west coast): ANSP 153379, 6, 100.7–168.4; ANSP 153380, 207.5; ANSP 153382, 102.4; Andaman Sea: ANSP 153381, 138.0.

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102(3), 1989, pp. 586–589

PARASPADELLA ANOPS, NEW SPECIES, FROM SAGITTARIUS CAVE GRAND BAHAMA ISLAND, THE SECOND TROGLOBITIC CHAETOGNATH

Thomas E. Bowman and Robert Bieri

Abstract.—*Paraspadella anops* is described from a single specimen collected in Sagittarius Cave, Grand Bahama Island. It lacks eyes and body pigmentation, and is the first fully troglobitic chaetognath discovered. In morphological details it closely resembles *P. schizoptera* (Conant), but is much slenderer than the latter. The separation of *Paraspadella* Salvini-Plawen, with two pairs of lateral fins, and *Gephyrospadella* Salvini-Plawen, with one pair, is rejected, since in the former the two pairs of fins are continuous in young specimens and only separated at sexual maturity by lateral growth of the vaginas. *Gephyrospadella* is reduced to a synonym of *Paraspadella*.

Until the discovery of the species described herein, the only chaetognath reported to be troglobitic was *Spadella ledoyeri* Casanova, 1986, from a marine cave about 15 km east of Marseille, France. In contrast to *Paraspadella anops*, however, *S. ledoyeri* has well developed eyes having "grand dêveloppement de la tache pigmentaire," which Casanova considered an adaptation to the reduction or absence of light in the interior of the cave. Casanova said nothing about the presence or absence of body pigment in *S. ledoyeri*.

Spadella equidentata Casanova, 1987, from 452 m in the Gulf of Cadiz, south of Portugal, was described as having not a trace of eyes, even after staining with methylene blue. However, Casanova (1987) remarked that the absence of eyes required confirmation.

The new species described herein is the first truly troglobitic chaetognath that lacks both eyes and body pigment.

Spadellidae Tokioka, 1965
Paraspadella Salvini-Plawen, 1986

Type species.—*Spadella schizoptera* Conant, 1895a (original designation).

Paraspadella anops, new species
Figs. 1–3

Material.—Bahamas, Grand Bahama Island, Sweeting's Cay, Sagittarius Cave (26°37′N, 77°53′W), leg. Dennis Williams and Jill Yager, 17 Dec 1987, holotype, USNM 120108.

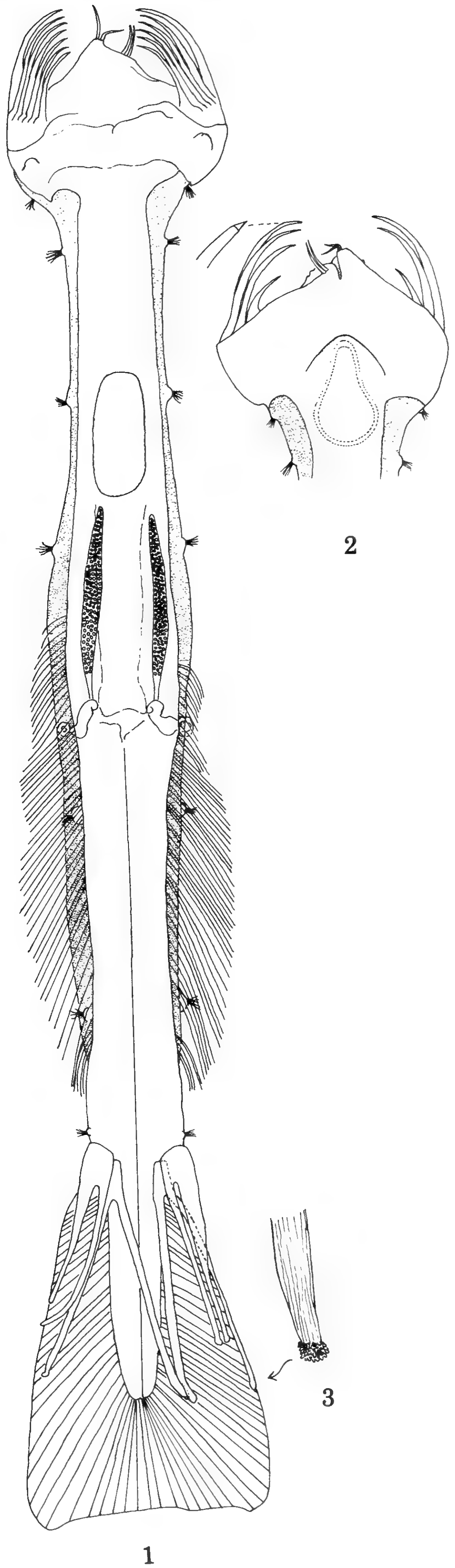
Etymology.—From the Greek "an-" (without) + "ops" (eye), alluding to the absence of eyes.

Description.—Total length, excluding tail fin, 3.55 mm. Length of tail 1.75 mm = 49.3% of total length. Eyes and body pigment totally lacking. Head about 1.4× as wide as long, about twice as wide as trunk and 2.7× as wide as tail. Grasping spines 10 on each side, each with tip set off by suture. Anterior teeth two on each side, elongate. Posterior teeth lacking. Corona ciliata pyriform, length about 1.6× greatest width, which is near posterior end. Collarette extending from posterior end of head to anterior insertion of tail fin. Lateral margins of collarette of trunk with four pairs of sensory tufts, of tail with three pairs. Anterior intestinal diverticula not evident in the undissected specimen. One pair of lateral fins, completely rayed, extending from distance equal to body width anterior to beginning of tail to short distance anterior to attachment of adhesive organs; fin width increasing posteriorly to maximum slightly posterior to fin midlength, thereafter decreasing. Tail fin beginning just posterior to insertion of adhesive organs; lateral margins nearly straight; posterior margin, which appears somewhat frayed, slightly concave.

Adhesive organs inserted on ventral surface of tail, each with four slender fingers. Outer two and inner two fingers each with common base. Outer two fingers subequal, about half length of tail fin; inner two fingers with inner member slightly longer, about two-thirds length of tail fin, reaching posterior margin of tail. Fingers longitudinally striated; tips of most fingers eroded, but one relatively undamaged tip covered with small papillae (Fig. 3).

Ventral ganglion oval, occupying middle one-fifth trunk. Ovaries immature, extending slightly anterior to 4th pair of sensory tufts. Transverse musculature appears to extend from posterior end of head to posterior margin of ventral ganglion.

Comparisons.—Of the known species of *Paraspadella, P. schizoptera* (Conant, 1895) most closely resembles *P. anops.* The two species agree in the numbers of grasping spines and anterior teeth; both have pyriform coronae ciliatae, and the number, form, and arrangement of the fingers of the adhesive organs are identical. However, *P. schizoptera* has well developed eyes and is heavily pigmented compared with most other chaetognaths (Feigenbaum 1976). It is also a stockier species than the very slender *P. anops,* whose length (excluding the tail fin) is about 9.5 × its greatest trunk width. The length : width ratio of *P. schizoptera* in published illustrations is as follows: 6.5



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Figs. 1–3. *Paraspadella anops*: 1, Habitus, ventral (not all 10 pairs of grasping spines shown; many fin rays omitted); 2, Head, dorsal; 3, Tip of finger of adhesive organ.

(Conant 1895a, fig. 6, 3.5 mm specimen), 7.8 (Owre 1963, fig. 1a, 1.7 mm specimen), 7.9 (Owre 1972, pl. 2, fig. 1, 3.8 mm specimen), 5.3 (Feigenbaum 1976, fig. 2f, 1.4 mm specimen).

Because of these differences, it is our subjective opinion that *P. anops* merits recognition as specifically distinct from *P. schizoptera,* but the latter is clearly the ancestor of our new species.

The genera of Spadellidae.—Prior to Salvini-Plawen's two new genera, the family Spadellidae Tokioka, contained only the genus *Spadella,* although three species-groups corresponding to the three genera recognized by Salvini-Plawen had been proposed. Salvini-Plawen (1986) assigned the 13 then known species of *Spadella* to 3 genera: *Spadella* Langerhans, 1880 (type species *Sagitta cephaloptera* Busch, 1851), one pair of lateral fins, no adhesive organs; *Gephyrospadella,* new genus (type species *Spadella pulchella* Owre, 1963), one pair of lateral fins, adhesive organs present; *Paraspadella,* new genus (type species *Spadella schizoptera* Conant, 1895a), two pairs of lateral fins, adhesive organs present.

We agree that the presence or absence of adhesive organs is significant at the generic level, but we have reservations about the supposed two pairs of lateral fins. Illustrations of *Paraspadella schizoptera* show specimens with two pairs (Conant 1895a, Owre 1972) and one pair (Owre 1963, Feigenbaum 1976) of lateral fins. Where there are two pairs, the gap between them is much smaller than in species of *Sagitta,* in which the anterior and posterior fins are widely separated. In *P. schizoptera* the fins are either continuous or separated only by the width of the female gonopore and vagina. It appears that the lateral fins are single in sexually immature individuals, but with the development of sexual maturity they become separated into anterior and posterior parts by lateral growth of the vagina. This slight separation scarcely warrants the recognition of two pairs of fins.

This observation leads us to combine Salvini-Plawen's proposed new genera, *Gephyrospadella* and *Paraspadella,* since they differ only in the supposed number of paired lateral fins. Acting as first revisors (ICZN Article 24), we may select one of the names. Salvini-Plawen did not give the derivation of his new generic names, but it is obvious the "Gephyro" means "bridge" and "Para" means "near." Salvini-Plawen's fig. 3 shows *Geophyrospadella* bridging the evolutionary pathway between *Spadella* and *Paraspadella.* Combining the new genera eliminates the bridge, hence we select *Paraspadella* rather than *Gephyrospadella.* This act reduces the number of genera of Spadellidae to two: *Spadella,* without adhesive organs, and *Paraspadella,* with adhesive organs.

Habitat.—A detailed description of Sagittarius Cave is given by Cunliffe (1985). It is an anchialine cave beneath the small island of Sweeting's Cay at the east end of Grand Bahama Island. The single specimen of *P. anops* was found swimming in the water column in an area completely devoid of light, more than 100 m inward from the surface entrance to the cave. The salinity was 35‰. Associated fauna include remipedians, ostracodes, amphipods, isopods, mysidaceans, thermosbaenaceans, and cave fishes.

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A REVIEW OF THE BEACH FLIES OF THE CARIBBEAN AND GULF OF MEXICO (DIPTERA: CANACIDAE)

Wayne N. Mathis

Abstract.—The beach flies (Diptera: Canacidae) of the Caribbean and Gulf of Mexico, with focus on the species of Belize (Central America), are reviewed. The faunas from the Caribbean and Gulf of Mexico comprise four genera and seven species as follows: *Canacea* Cresson (*C. macateei* Malloch), *Nocticanace* Malloch (*N. texensis* (Wheeler); *N. wirthi,* new species; *N. panamensis,* new species), *Paracanace* Mathis & Wirth (*P. aicen* Mathis & Wirth; *P. lebam* Mathis & Wirth), and *Procanace* Hendel (*P. dianneae* Mathis). Keys and a diagnosis are provided for each genus and most species, and for *Nocticanace, Paracanace,* and *Procanace* a key to the species groups on a world basis is furnished. In addition, the *texensis* group of the genus *Nocticanace* is revised. Several structures of each new species are illustrated to facilitate their identification.

In the published literature on the dipterous family Canacidae, more commonly known as beach flies, no mention is made of collection records from the Caribbean or Gulf of Mexico before 1950. Since then, the record is limited primarily to descriptions of a few new species (Wirth 1975). For individual countries that are a part of this region, the paucity of information is even more acute—usually none exists. Thus for a country like Belize, which is a focus of this paper, there are no records of beach flies, either under that geopolitical name or its predecessor, British Honduras. Although no species or collection records have been published from Belize, the occurrence of a few species was expected because genera such as *Canacea* Cresson and *Nocticanace* Malloch include species with distributions in adjacent countries (Wirth 1975). Like most projects on the systematics of Diptera, however, especially those concerned with the neotropics, many of the observations and discoveries reported here were not anticipated. To give greater meaning and perspective to these findings, the results are reported within the context of a faunal review of the beach flies of the Caribbean and Gulf of Mexico.

The impetus for this project resulted from field work on the insects of mangroves, sometimes called the mangal (Tomlinson 1986), that are associated with Belizean cays, especially those within the Stann Creek District. With funding from the Caribbean Coral Reef Ecosystems Program (CCRE), field work has been conducted on the mangrove habitats of Twin Cays, with reconnaissance work on several of the nearby cays as well. On five field trips to these cays, I have made particular effort to collect specimens of the family Canacidae. This study also includes recently collected specimens from field work that I conducted in Cuba (1984), Dominica and St. Vincent (1989), and Florida (1989). In addition, W. W. Wirth made special effort to collect beach flies on visits to Antigua, Dominica, Jamaica, and Puerto Rico and has graciously made these specimens available. A total of three species was collected and is reported here from Belize. This brings the total number of beach-fly species from the Caribbean and Gulf of Mexico to seven.

Most of the specimens that were studied in conjunction with this paper are in the collections of the Smithsonian Institution (USNM). Others, especially primary types, were borrowed from other institutions. These institutions and their acronyms, as used in the text, and their respective curators are as follows: CAS—California Academy of Sciences, San Francisco, California (Dr. Paul H. Arnaud, Jr.); BDAF—Department of Agriculture and Fisheries, Botanical Garden, Paget, Bermuda (Dr. Daniel J. Hilburn); IZAC—Intituto de Zoologia, Academia de Ciencias, Havana, Cuba (Mr. Jorge L. Fontenla).

For each genus and species treated in this review, a synonymy, diagnosis, the known distribution, and a remarks section are provided. In the synonymies, only the literature that is pertinent to the Caribbean and Gulf regions or the species' nomenclatural history is cited. Specific collection data, except for the *texensis* group of the genus *Nocticanace,* are cited only for Belizean specimens. The *texensis* group is more comprehensively revised to include complete descriptions and a listing of all specimens examined. The descriptive format for the new species follows Mathis & Wirth (1978) and Mathis (1982, 1988). The illustrations of the male terminalia, especially the lateral views of the surstylus, were drawn from flattened, slide-mounted structures to ensure uniform views. In some specimens, the apex of the surstylus has a tendency to curve inward ventrally, partially obscuring the shape of that structure from a lateral view. A more detailed account of the morphology and higher classification of Canacidae can be found in Mathis (1982) and Wirth (1987). Two venational ratios are used commonly in the descriptions. Costal Vein Ratio: The straight line distance between the apices of R_{2+3} and R_{4+5}/distance between the apices of R_1 and R_{2+3}. M Vein Index: The straight line distance along vein M between crossveins (dm-cu and r-m)/distance apicad of dm-cu.

Key to Genera of Canacidae from the Caribbean and Gulf of Mexico

1. Lateroclinate fronto-orbital setae four or more; fore femur bearing row of usually from four to five spinelike setae along apical one-half of anteroventral surface; apical one-third of arista bare; two supra-alar setae .... *Canacea* Cresson
– Lateroclinate fronto-orbital setae three; fore femur lacking row of spinelike setae; arista evenly haired throughout length; one supra-alar seta 2
2. Intrafrontal setae absent, although anterior one-third of frons occasionally with scattered setulae .... *Procanace* Hendel
– Intrafrontal setae present, one or more pairs in addition to any setulae 3
3. One intrafrontal seta present; postocellar setae either much reduced or lacking .... *Nocticanace* Malloch
– Two intrafrontal setae present; postocellar setae well developed, proclinate and slightly divergent .... *Paracanace* Mathis & Wirth

Genus *Canacea* Cresson

Canacea [lapsus].—Malloch, 1924:52 [unavailable; see Mathis, 1982, for discussion].

Canacea Cresson, 1924:164. Type species: *C. macateei* Malloch, by original designation [Cresson validated Malloch's name as an indication].—Mathis, 1982:4–7 [review].

Canace [in part].—Wirth, 1951:259–265 [review]; 1965:733 [nearctic catalog]; 1970:397–403 [revision]; 1975:1 [neotropical catalog].—Wheeler, 1952:90–91 [discussion].

Diagnosis.—Moderately small to moderately large beach flies, length 2.0 to 4.5 mm.

Head: Mesofrons distinct from parafrons, shiny, very thinly microtomentose, bearing from three to five large, proclinate setae along lateral margin, mesofrons bare of setae; parafrons microtomentose, appearing dull; postocellar setae subequal in length to ocellar setae and with similar orientation; four large, lateroclinate, fronto-orbital setae; arista variable, usually with apical one-fourth to one-third bare of setulae, stylelike, some species with minute setulae extended nearly to apex but not appearing plumose; anaclinate genal setae two; anteroclinate genal seta one.

Thorax: Dorsocentral setae 4 (1 + 3), all subequal in size; acrostichal setae conspicuous, arranged in 4 irregular rows anteriorly, becoming more regular posteriorly, middle rows with setulae slightly larger and with large pair of prescutellar setae; lateral scutellar setae 2 pairs and with several setae dorsally; supra-alar setae 2, anterior seta only slightly smaller than posterior seta; 2 notopleural setae; color of pleural setulae variable, usually black, all large setae black; propleuron bare of setulae; 1-2 large, anepisternal setae; katepisternal setae present; fore femur with row of 3–12 stout, spinelike setae anteroventrally; hind tibia lacking apical seta anteroventrally; apical section of vein M straight.

Abdomen: Female epiproct broad basally, roughly triangular to nearly ellipsoidal, cerci as two parallel-sided narrow processes, each with one long, stout, apical seta; male surstylus with anteriorly curved hook.

Discussion.—*Canacea* is a New World genus of four species that are primarily tropical in distribution. Mathis (1982) last reviewed the genus.

Canacea macateei Malloch
Figs. 1–12

Canacea macateei Malloch, 1924:52.—Cresson, 1924:164 [discussion]; 1936:265 [discussion].—Johnson, 1925:276 [list].—Mathis, 1982:7 [review].

Canace snodgrassii [misidentification, in part].—Johnson, 1910:807 [list].—Wirth, 1951:260 [synonymy]; 1965:733 [nearctic catalog].

Canace macateei.—Malloch, 1933:5 [note].—Curran, 1934:356 [status].—Wheeler, 1952:90–91 [distribution, key].—Wirth, 1970:399 [resurrection from synonymy, figure of male terminalia].—Teskey and Valiela, 1977:545–547 [description of larva and puparium, natural history].

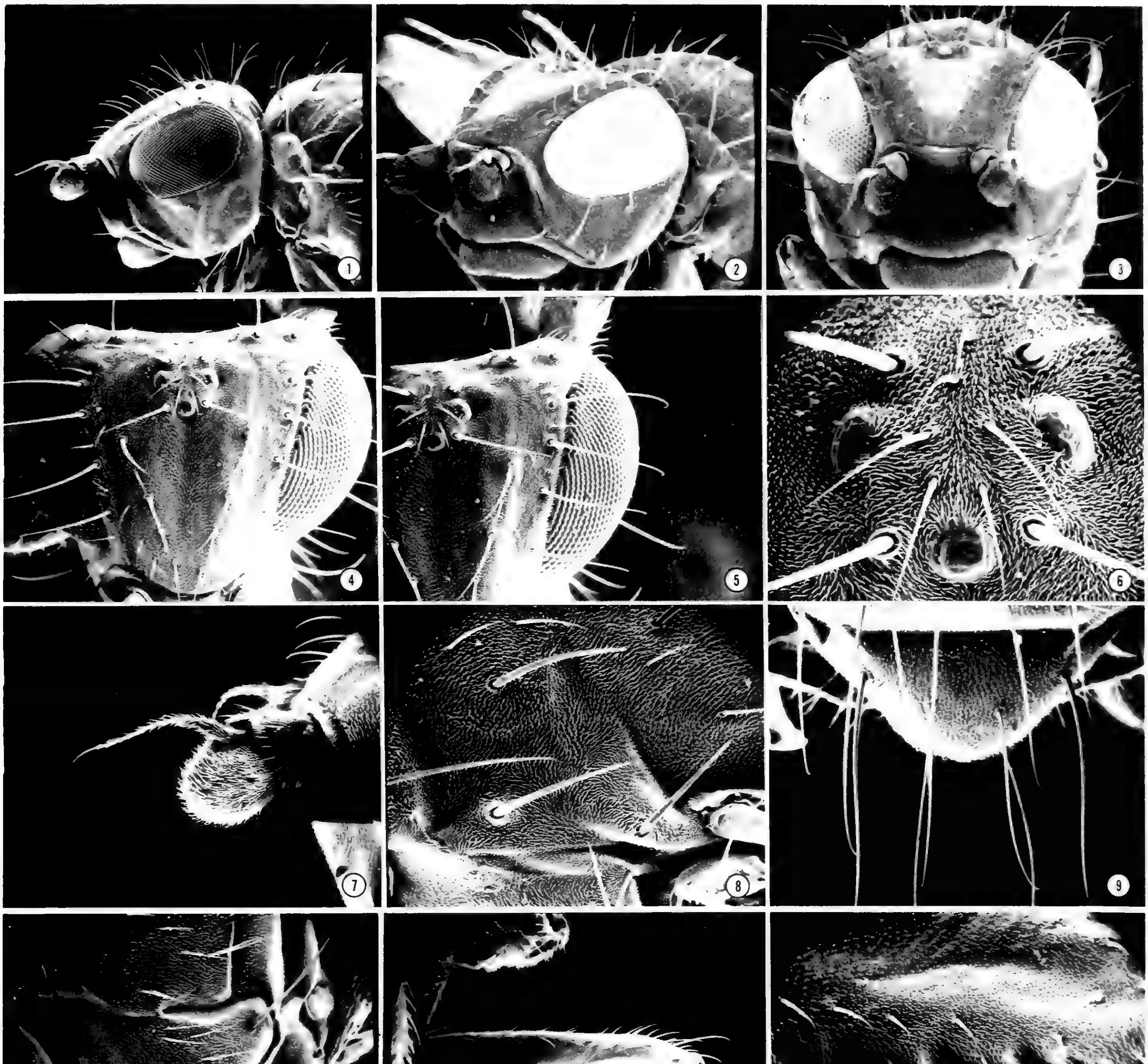
Specimens examined.—Belize. Stann Creek District: Twin Cays (Aanderaa Flats), 7–19 Nov 1987, W. N. & D. Mathis (28 ♂, 14 ♀; USNM); Twin Cays (S end of West Island), 17 Nov 1987, W. N. & D. Mathis (1 ♂; 1 ♀; USNM).

Distribution.—Canada (New Brunswick, Prince Edward Island) and United States (Atlantic and Gulf coasts from Maine to Texas), south to Cuba and Belize.

Natural history.—Teskey & Valiela (1977) successfully reared this species from larvae and puparia that were collected on mats of blue-green algae in Great Sippewissett marsh on Cape Cod, Massachusetts. Larvae of *C. macateei,* along with those of Dolichopodidae, were the principal contributors to the biomass of invertebrates in the algal mats. Pupae were quite common, and the pupal stage is very brief, perhaps no more than two to three days. Adults were observed to aggregate, especially at night, on the tops of grass-covered dunes.

In Belize, we collected adults by sweeping an aerial net just above mats of blue-green algae that occurred along the mud banks of brackish pools. The surface of the mud banks, which is water covered only at higher tides, is broken by deep cracks that have divided the bank into irregularly shaped mud plates that are 15–25 cm in diameter. The algal mats were comparatively thick, and as a protective covering, they helped keep the underlying mud moist.

Remarks.—The species of *Canacea* are



Figs. 1–12. Scanning electron micrographs of *Canacea macateei*: 1, Head, lateral view; 2, Head, fronto-oblique view; 3, Head, anterior view; 4, Frons, dorsal view; 5, Fronto-orbital setae, dorsal view; 6, Ocellar triangle, dorsal view; 7, Antenna, lateral view; 8, Notopleuron and setae, lateral view; 9, Scutellum, dorsal view; 10, Katepisternum and setae, lateral view; 11, Left foreleg, anterior view; 12, Enlargement of left fore femur and tibia showing anteroventral, spinelike setae, anterior view.

quite similar externally but can be distinguished by the structures of the male terminalia and the position, number, and color of certain setae. Specimens of *C. macateei* can be distinguished from congeners by the following combination of characters: fore femur with a row of from three to five stout, anteroventral setae; the setulae of the pleural sclerites are black; specimens are generally larger, over 2.50 mm in length; and the surstylus of the male terminalia has the stem of the hook wider than long.

Genus *Nocticanace* Malloch

Nocticanace Malloch, 1933:4. Type species: *N. peculiaris* Malloch, by original designation.—Wirth, 1951:269–274 [revision]; 1965:734 [nearctic catalog]; 1975: 2–3 [neotropical catalog].

Diagnosis.—Small to medium-sized beach flies, length 1.8 to 3.7 mm; general coloration grayish black.

Head: Intrafrontal setae one pair; postocellar setae either absent or much reduced, less than one-fourth length of ocellar setae; ocelli arranged to form an isosceles triangle, distance between posterior ocelli greater than that between either posterior ocellus and the anterior ocellus. Epistomal margin sinuate; clypeus low, width subequal to length of antenna. Two long anaclinate genal setae; anteroclinate genal seta moderately well developed, at least one-half length of larger anaclinate genal setae. Palpus grayish black, bearing one to several long setae, each seta two to three times greatest width of palpus.

Thorax: Anepisternum with scattered setulae; proepisternal seta absent; katepisternal seta present, well developed. Legs entirely dark colored, grayish black; fore femur bearing from four to six long and evenly spaced setae along posteroventral margin, length of setae at least equal to and usually greater than width of femur.

Discussion.—In preparing the following key to species groups, I have examined most species of the genus. The key, however, should still be considered preliminary, and I invite the critique and comment of users, as eventually I plan to review the remaining genera of Canacidae in a paper similar to Mathis (1982). The new species that are described below belong to the *texensis* group, which is also characterized and its species revised.

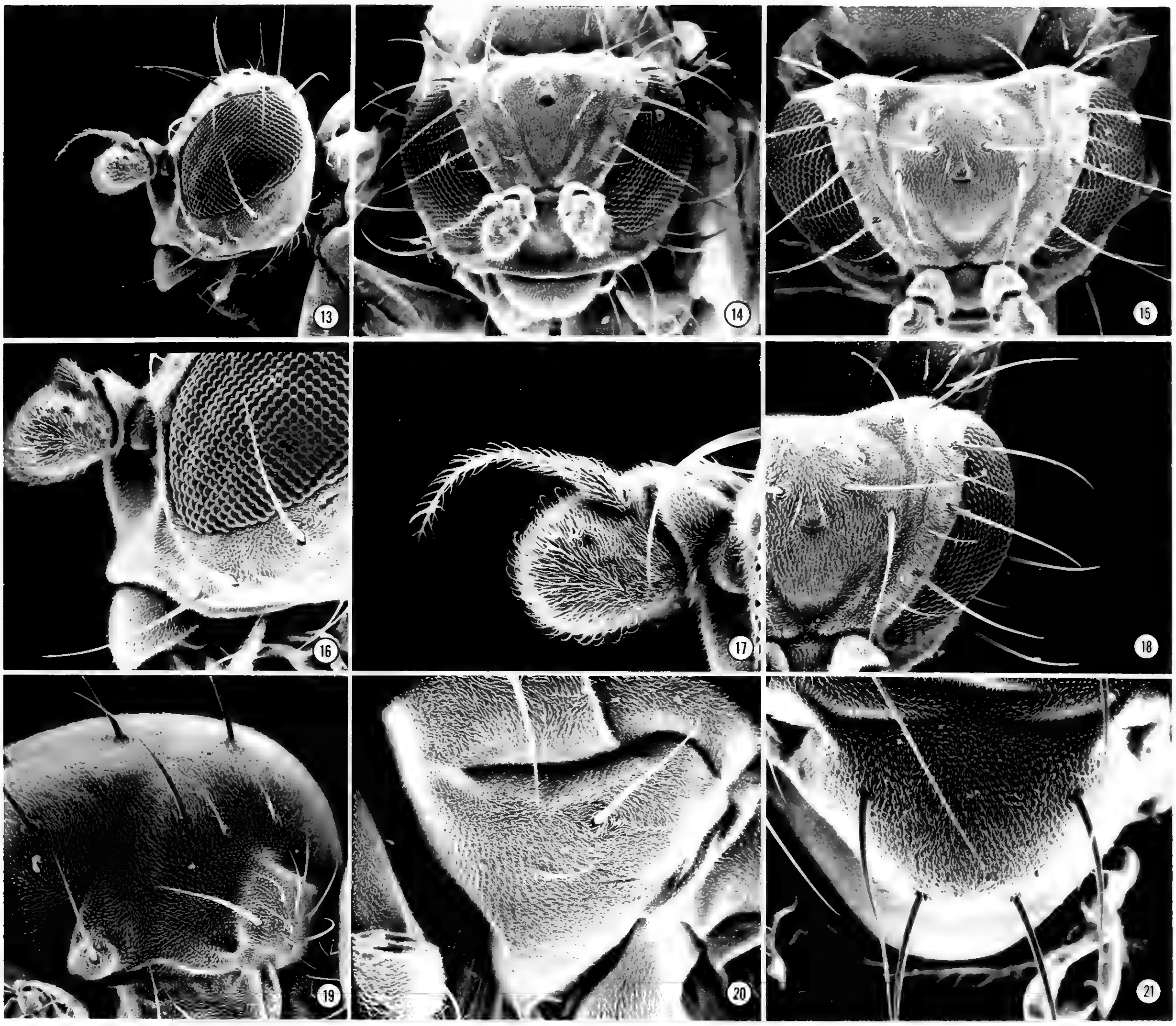
Annotated Key to Species Groups of the Genus *Nocticanace*

1. Anterior notopleural seta absent .. 2
– Anterior notopleural seta present .. 3
2. Apical scutellar setae distinctly curved anaclinate ... the *pacifica* group [19 species; Old World and Oceania]
– Apical scutellar setae straight to very slightly curved .... the *texensis* group [3 species; Caribbean, Gulf of Mexico, Atlantic coast of southeastern United States]
3. Length of apical section of vein CuA_1 twice or more length of crossvein dm-cu .... the *galapagos* group [8 species; Galápagos Islands and southwestern North America]
– Length of apical section of vein cuA_1 subequal to length of crossvein dm-cu 4
4. Apical scutellar setae distinctly anaclinate .... the *ashlocki* group [1 species, *N. ashlocki* Wirth; Galápagos Islands]
– Apical scutellar setae not anaclinate .... the *chilensis* group [1 species, *N. chilensis* (Cresson); Chile (there are numerous undescribed species in this group)]

The *texensis* Group

Diagnosis.—Acrostichal setae lacking; apical scutellar setae nearly straight in lateral view, slightly convergent in dorsal view, but not distinctly curved upward; anterior notopleural seta lacking, only a posterior seta present; proepisternal seta(e) present; mid femur of male lacking comblike row of setae; hind basitarsomere lacking spinelike basoventral setae. Wing with length of apical section of vein CuA_1 long, about twice length of crossvein dm-cu; M vein index 0.42–0.49.

Discussion.—Until now, the only included species in the *texensis* group was *N. texensis* (Wheeler). The two new species added here are very similar and are very closely related to *N. texensis*. The three species together are the only representatives of the



Figs. 13–21. Scanning electron micrographs of *Nocticanace texensis*: 13, Head, lateral view; 14, Head, anterior view; 15, Head, dorsal view; 16, Gena and setae, lateral view; 17, Antenna, lateral view; 18, Fronto-orbital setae, dorsal view; 19, Right notopleuron and setae, lateral view; 20, Left katepisternum and setae, lateral view; 21, Scutellum, dorsal view.

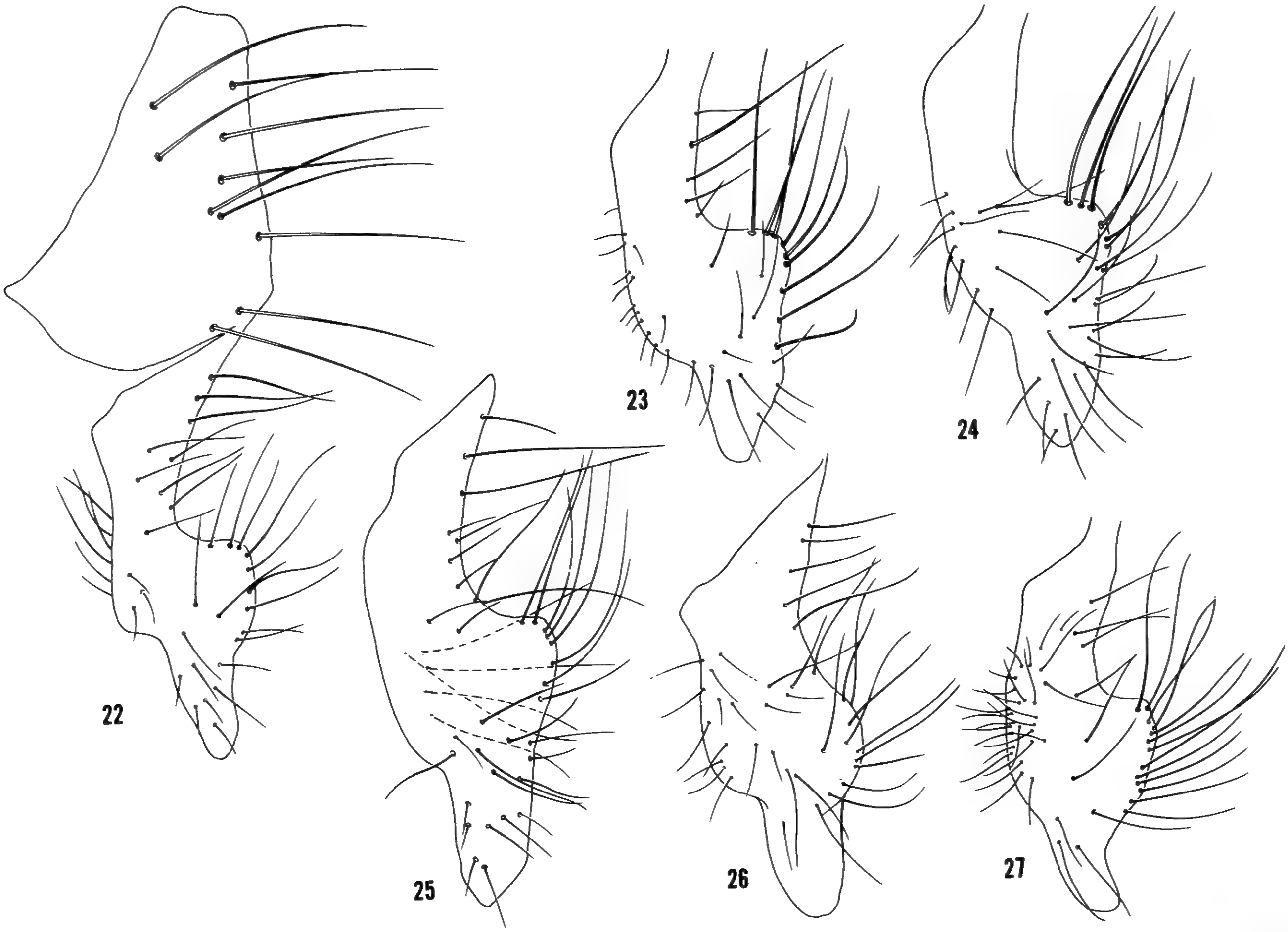
genus *Nocticanace* that occur on beaches of the Atlantic Ocean (primarily within the Caribbean Sea and Gulf of Mexico). Other species of *Nocticanace* are found along coasts of the Indian and Pacific oceans. The species of the *texensis* group probably arose from a single lineage that originally came from the Pacific Ocean and then penetrated into and radiated within the Caribbean Sea and Gulf of Mexico.

As there are only three known species in the *texensis* group, I have not provided a key to distinguish between them. The diagnoses, descriptions (only *N. texensis* is completely described; the others are compared to it), and figures (Figs. 13–29) adequately outline characters to distinguish between them and other congeners. The only distinguishing characters between the three species of the *texensis* group that I have found are those of the male terminalia.

Nocticanace texensis (Wheeler)
Figs. 13–27

Canaceoides texensis Wheeler, 1952:92.
Nocticanace texensis.—Wirth, 1954:62 [generic combination]; 1965:734 [nearctic catalog]; 1975:3 [neotropical catalog].

Diagnosis.—Small to moderately small beach flies, length 1.60 to 2.95 mm (holo-



Figs. 22–27. External male terminalia of *Nocticanace texensis*: Variation in shape of the surstylus from same and different localities, lateral views: 22, Belize, Stann Creek District, Carrie Bow; 23, USA, North Carolina, Wrightsville; 24, USA, North Carolina, Wrightsville; 25, Mexico, Tabasco, Paraiso (5 km N); 26, Antigua, Dutchman Bay; 27, Dominica, David Bay.

type 2.15 mm). Coloration generally brown dorsally and gray laterally.

Head: Frons generally brown to olivaceous or slightly charcoal brown, coloration of frons uniform or ocellar triangle more grayish, and fronto-orbits charcoal gray. Ocellar setae divergent, lateroclinate; intrafrontal setae anteroclinate, slightly convergent; ocellar area with three or four smaller setulae. Face, clypeus, and gena (to an extent) whitish, with faint tinges of blue or gray, gena becoming darker posteriorly, more charcoal gray. Orientation and size of genal setae as follows (anterior to posterior setae): 1st seta large, anteroclinate; two large anaclinate setae with one, rarely zero or two anaclinate setulae between larger anaclinate setae; anaclinate setula about one-third length of larger setae.

Thorax: Mesonotum from dorsal view mostly brown to olivaceous brown, darker around anterior margins; postpronotum, anterior half of notopleuron, and to a lesser degree the posterior fourth of scutum, and scutellum gray; coloration of thorax in lateral view brown dorsally, becoming gray ventrally around area of notopleuron (in some specimens just above, others at or below notopleuron), remainder of pleural areas mostly unicolorous, gray. Notopleuron bearing only one seta, inserted posteriorly; anepisternum with three large setae and from three to five smaller setulae between larger ones, larger setae with insertions and orientations as follows: posterior seta, usually the largest, with posteroclinate orientation, ventral seta, usually the next largest, with declinate orientation, dorsal seta smallest (not much larger than setulae) and with anaclinate orientation; one large katepisternal seta and one or two smaller setulae inserted ventrad or anteroventrad. Fore femur with four or five long setae along posteroventral margin and four or five shorter setae posterodorsally; mid tibia bearing apicoventral spinelike seta, length about equal to tibial width; hind basitarsomere lacking basoventral pair of larger setae; legs mostly concolorous, gray to dark gray apically. Wing generally lightly infumate, brownish; costal vein ratio averaging 0.13 (holotype 0.15); M vein index averaging 0.43 (holotype 0.49); apical section of vein CuA_1 slightly more than twice length of crossvein dm-cu.

Abdomen: Dorsum mostly olivaceous brown, gray laterally and ventrally. Male terminalia (Figs. 22–27) as follows: posterior margin of surstylus densely setulose, posterior half of surstylus in lateral view roughly triangular, distinctly angulate to form a large and wide posterior projection and a tapered, more slender process ventrally (sometimes curved inward), anterior margin with a subapical emargination (see remarks section below for discussion of variation).

Type material.—The holotype male is labeled "Galveston[,] Tex[as] 9.13.50 [handwritten]/M. R. Wheeler Collectors/Holotype Canaceoides texensis Wheeler 1952 [red; handwritten]." The allotype female (not examined) is reported to bear the same locality label data as the holotype. The holotype is double mounted (glued to a paper point), is in excellent condition (the abdomen has been removed, dissected, and the parts are stored in an attached plastic microvial), and is deposited in the California Academy of Sciences.

Other specimens examined.—Antigua. Dutchman Bay, 7 Jan 1965, W. W. Wirth (4 ♂; USNM). Belize. Stann Creek District: Carrie Bow, 4 Mar 1984, 2 Jun 1985, 15–27 Jan 1987, W. N. Mathis, C. Feller (18 ♂, 9 ♀; USNM). Dominica. Calibishie (sea shore), 27 Feb–22 Mar 1965, 1989, W. N. Mathis, W. W. Wirth (15 ♂, 3 ♀; USNM); Coulibistri, beach, 21 Mar 1989, W. N. Mathis (23 ♂, 10 ♀; USNM); Layou River (mouth), 9 Jan 1965, W. W. Wirth (1 ♀; USNM); Macoucheri (sea shore), 1 Feb 1965, W. W. Wirth (1 ♀; USNM); Pagua Bay, 18 Feb 1965, W. W. Wirth (6 ♂, 5 ♀; USNM); Rosalie (cobble beach), 23 Mar 1989, W. N. Mathis (7 ♂, 4 ♀; USNM); Soufrière Bay, 24 Mar 1989, W. N. Mathis (9 ♂, 6 ♀; USNM); St. David Bay (sea shore), 23 Jan 1965, W. W. Wirth (15 ♂, 10 ♀; USNM). Mexico. Tabasco Province: Paraiso (5 km E), 6 May 1985, W. N. Mathis, A. Freidberg (26 ♂, 25 ♀; USNM). St. Vincent. Buccament Bay, 25–28 Mar 1989, W. N. Mathis (7 ♂, 4 ♀; USNM); Cumberland Bay, 28 Mar 1989, W. N. Mathis (4 ♂; USNM); Wallilabou (beach), 27 Mar 1989, W. N. Mathis (8 ♂, 4 ♀; USNM). United States. North Carolina: Wrightsville Beach (light trap), 3–7 Sep 1953, R. H. Foote (9 ♂, 23 ♀; USNM).

Distribution.—East (North Carolina south) and Gulf coasts of North America, West Indies (Antigua, Dominica, and St. Vincent), and Caribbean coast of Mexico and Belize.

Natural history.—All of the specimens from Belize were collected on Carrie Bow Cay, formerly Ellen Cay, which is a highly disturbed, vegetated sand cay that is about 18 km off the coast of Hopkins, Stann Creek District. The cay is small, 100 by 40 m, and the former woodland, mostly red mangrove, has been cleared. Twenty-two species of plants have been recorded from Carrie Bow, including a few that have been introduced. Stoddart et al. (1982) and a more recent paper by Rützler and Ferraris (1982) provide more extensive information on Carrie Bow and its habitats.

The specimens of *N. texensis* were collected by sweeping an aerial net with a fine-meshed bag immediately over and between rocks and exposed coral on the surrounding beach, which is mostly sand covered, especially on the north, east, and south sides.

Remarks.—Externally, this species is very similar to *N. wirthi* but can be distinguished from it and other congeners by the following characters: anterior notopleural seta absent; acrostichal setae absent; apical scutellar setae nearly straight in lateral view, not distinctly curved dorsally (anaclinate); and shape of the male terminalia, especially the unique surstylus (see figures).

The shape of the surstylus is quite similar to that found in males of *N. arnaudi* Wirth (the *galapagos* group), but specimens of the latter are usually larger (3–3.5 mm), are much darker brown dorsally with the dark coloration extended ventrally to the dorsal third of the anepisternum, and the notopleuron usually bears an anterior and posterior seta, although the latter seta is usually much better developed.

The shape of the surstylus also differs slightly from locality to locality (see Figs. 22–27 from different localities), and I interpret this to be intraspecific variation, perhaps clinal in nature. The differences found in populations from the Lesser Antilles, however, especially those from Dominica, could represent interspecific variation. The surstylus from a male collected in Antigua (Fig. 26), for example, appears to be somewhat intermediate between that found on Dominica (Fig. 27) and the more typical shape, as found in males from North Carolina, Texas, Mexico, and Belize (Figs. 22–25). Unfortunately no specimens are available from the Greater Antilles that could provide important evidence to help resolve this issue, and for the present, I prefer to recognize a single species.

Nocticanace wirthi, new species
Fig. 28

Nocticanace texensis [of authors, not Wheeler].—Wirth, 1954:61–62 [illustration of male terminalia]; 1965:734 [nearctic catalog].

Diagnosis.—As in the preceding species except as follows: small to moderately small beach flies, length 1.75 to 2.25 mm.

Abdomen: Male terminalia as follows (Fig. 28): surstylus in lateral view with two large, ventral lobes; posteroventral lobe wide, pointed anteroventrally, and densely setulose, especially along outer margin; anterior lobe blunt, thumblike, and setulose.

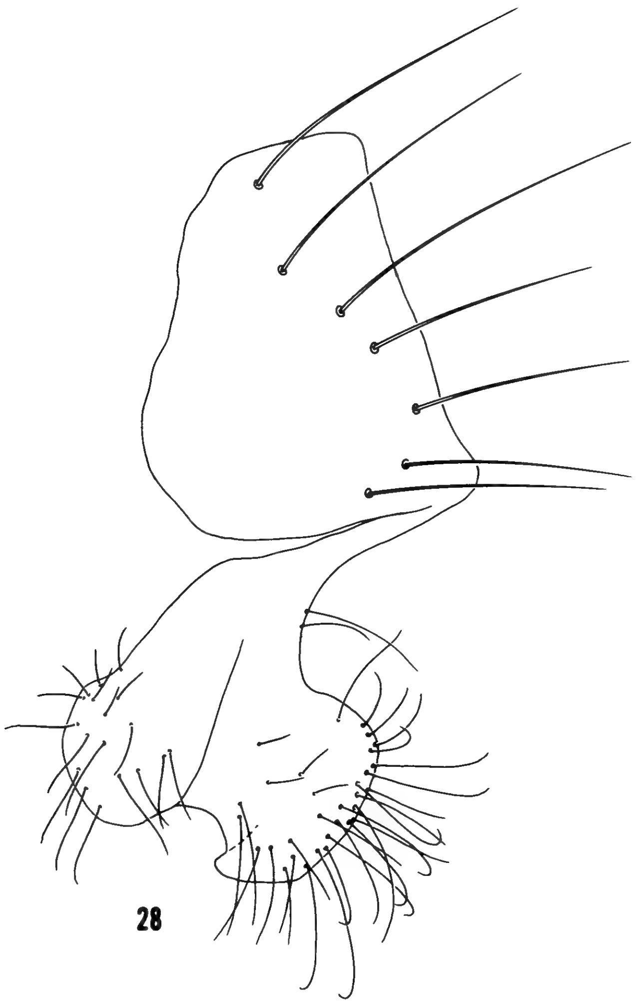
Type material.—The holotype male is labeled "Boyton Beach, Fl[orid]a [Palm Beach Co.]/WWWirth Collector/10 VIII 51 [10 Aug 1951] Intertidal rocks/♂/Nocticanace texensis (Wheeler) det WWirth [species name handwritten; black sub-border]/HOLOTYPE ♂ Nocticanace wirthi Mathis USNM [species name handwritten; red]." The allotype female and 14 paratypes (7 ♂, 7 ♀; CAS, USNM) bear the same locality label data as the holotype. Other paratypes are as follows: Cuba. Matanzas Province: Playa Larga, 1 May 1983, W. N. Mathis (3 ♂, 9 ♀; IZAC, USNM). Bermuda. Smith's Parish: Spittal Pond (intertidal rocks), 18 Nov 1987, N. E. Woodley (21 ♂, 25 ♀; BDAF, USNM). The holotype is double mounted (minute nadel in a cork block), is in good condition, and is in the Smithsonian Institution (USNM).

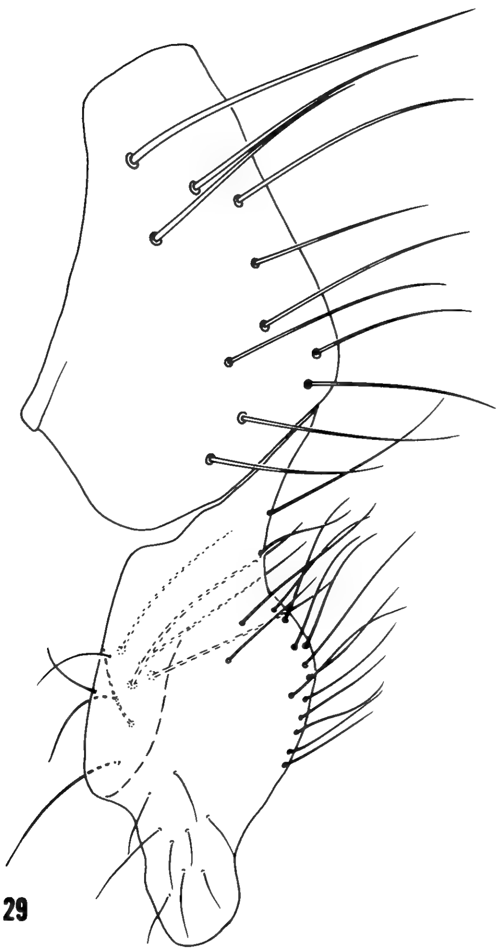
Distribution.—Bermuda, Cuba, and southern Florida.

Natural history.—Wirth (1954:62) reported that the type series was "... collected from a shelf of limestone rock about a hundred yards long on the Atlantic Ocean beach. The rock projected from the water only at low tide and was covered with a scanty growth of filamentous green algae." The specimens collected in Cuba were swept from a large limestone outcrop that extended into the sea. The limestone was deeply eroded, and the exposed surface had numerous sharp ridges.

Etymology.—It is a pleasure to name this species after Dr. Willis W. Wirth, who has contributed substantially to our knowledge of beach flies and who first illustrated this species.

Remarks.—This species is very similar to *N. texensis,* and the only distinguishing characters that I have found between these two species are those of the male terminalia,





Figs. 28–29. Lateral view of male terminalia: 28, *Nocticanace wirthi*; 29, *Noticanace panamensis*.

especially the bilobed shape of the surstylus (see description and figures). Externally the specimens are virtually impossible to separate from those of *N. texensis*.

Nocticanace panamensis, new species
Fig. 29

Diagnosis.—As in *N. texensis* except as follows: moderately small beach flies, length 2.0 mm (based on the single pinned ♀ paratype).

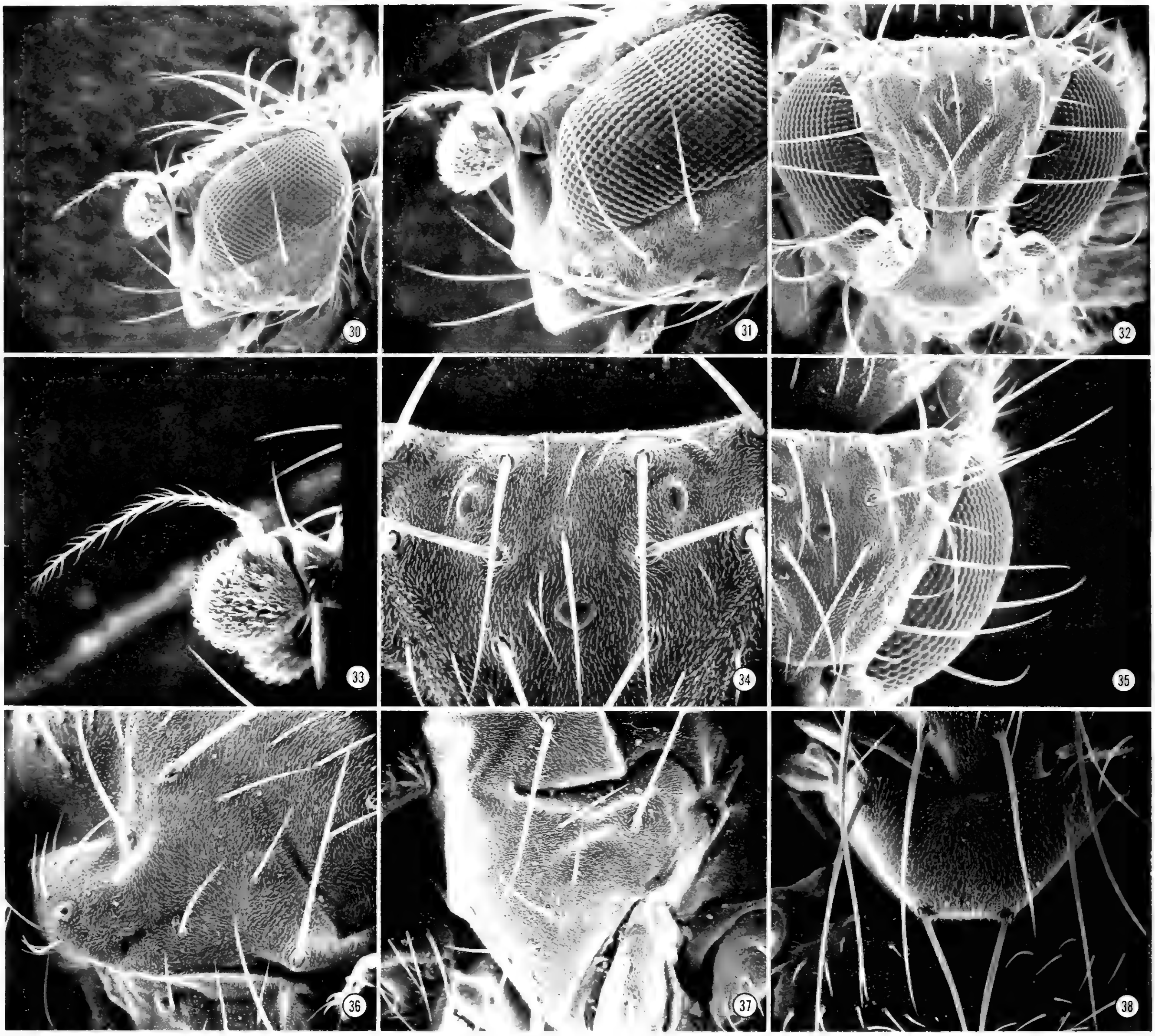
Abdomen: Male terminalia as follows (Fig. 29): surstylus in lateral view more or less rectangular, posterior margin conspicuously setulose; inner lobe not developed as a process, bearing several setulae along median surface; outer lobe a large, thumblike posteroventral process that bears several setulae.

Type material.—The holotype male is labeled "[Panama] Mojinga Swamp[,] Ft. Sherman, C. Z. Jan. 1953[,] F. S. Blanton ct. [collector] Nocticanace texensis (Wheeler) ♂ 5 ["5" is circled][handwritten]." The allotype female (double mounted) and three paratypes (3 ♀; USNM; slide mounted) bear the same label data as the holotype. The holotype is slide mounted in balsam (most body parts have been dissected and are separated) and is in the Smithsonian Institution (USNM).

Distribution.—Panama. Fort Sherman is located at the Caribbean mouth of the Panama Canal.

Etymology.—The specific epithet, *panamensis*, refers to the country of Panama, where the type series was collected.

Remarks.—Like *N. wirthi*, this species differs from *N. texensis* in characters of the male terminalia, especially the shape of the surstylus (see figures and description above).



Figs. 30–38. Scanning electron micrographs of *Paracanace hoguei*: 30, Head, lateral view; 31, Gena and setae, lateral view; 32, Head, dorsal view; 33, Antenna, lateral view; 34, Ocellar triangle, dorsal view; 35, Fronto-orbital setae, dorsal view; 36, Notopleuron and setae, lateral view; 37, Katepisternum and setae, lateral view; 38, Scutellum, dorsal view.

Genus *Paracanace* Mathis & Wirth

Paracanace Mathis & Wirth, 1978:524. Type species: *P. hoguei* Mathis & Wirth, by original designation.

Diagnosis.—Small to moderately small beach flies, 1.40 to 2.60 mm; general coloration whitish gray to brownish black.

Head: Intrafrontal setae two pairs; postocellar setae well developed, proclinate and very slightly divergent, subequal in length to intrafrontal setae; ocelli arranged to form isosceles triangle, with greater distance between posterior ocelli. Two to three large anaclinate genal setae; anteroclinate genal seta well developed, subequal in length to larger anaclinate genal setae; epistomal margin sinuate; clypeus low, width more than 4× height; palpus yellowish.

Thorax: Acrostichal setulae present, in about four rows, with a distinctly larger prescutellar pair; scutellar disc lacking setae; apical scutellar setae not anaclinate; anterior notopleural seta usually present (very weak or absent in one species); proepisternal seta(e) present; anepisternum with scattered setulae; katepisternal seta present. Femora and tibiae grayish black; tarsomeres yellowish brown to dark brown, becoming darker apically; mid femur of male with comblike row of setae; hind tibia lacking spinelike setae apically. Wing with length of apical section of vein CuA_1 twice or more that of crossvein dm-cu; vein M index 0.38.

Discussion.—Like *Canacea*, all of the described species of *Paracanace* occur in the Western Hemisphere, with primarily tropical or subtropical distributions (Mathis and Wirth 1978).

I have recognized two species groups within *Paracanace*. This arrangement adheres to the cladogram for the species of this genus that Mathis and Wirth (1978:535) published. The two species groups are characterized in the key that follows. All known Caribbean species belong to the *hoguei* group (Figs. 30–38).

Key to Species Groups of *Paracanace*

1. Fore femur of male with from three to four long setae along posteroventral surface, setal length subequal to 2× femoral width; mid femur of male bearing a posteroventral, comblike row of setae along entire length, setae at proximate one-fourth pale; costal vein between humeral crossvein and subcostal break usually bearing a row of long spinelike setae, setal length subequal or greater than width of 1st costal cell . . . . The *hoguei* Group
– Fore femur of male lacking three or four setae as described above; mid femur of male bearing a posteroventral comblike row of setae along distal one-half only; setae along anterior margin of wing much shorter, not more than one-half width of 1st costal cell . . . . . . The *maritima* Group

Key to Species of the *hoguei* Group

1. Three, dorsally curved, genal setae subequal in length; body strongly setose (Figs. 30–38) (Cocos Island. Costa Rica) . . . . *P. hoguei* Mathis & Wirth
– Middle, dorsally curved, genal seta about one-half length of setae on either side; body moderately setose 2
2. Surstylus broader on distal half, especially evident in lateral view; ventral, surstylar margin broadly truncate in lateral and posterior views; posterior margin of surstylus bearing distinct row of longer setae (Florida, Jamaica) . . . . *P. lebam* Mathis & Wirth
– Surstylus in lateral view swollen along anterior margin near middle, tapered ventrally to broadly rounded, ventral margin; posterior margin of surstylus lacking distinct row of longer setae; posteroventral angle of surstylus noticeably produced apically (Figs. 39, 40) (Belize, Cuba, Dominica) . . *P. aicen* Mathis & Wirth

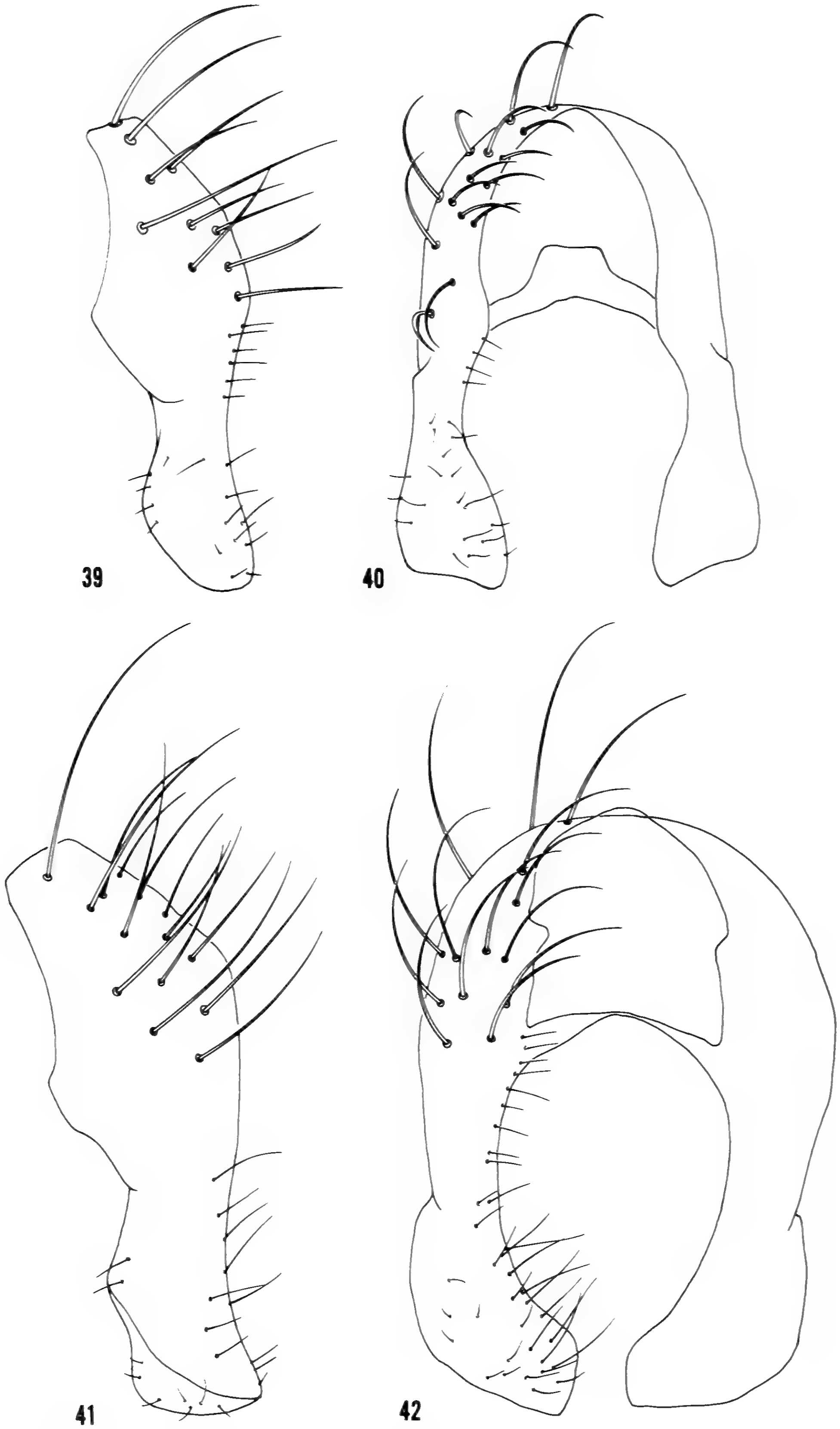
Paracanace aicen Mathis and Wirth
Figs. 39–42

Paracanace aicen Mathis & Wirth, 1978: 533.

Specimens examined.—Belize. Stann Creek District: Carrie Bow Cay, 15 Jan–2 Jun 1984–1987, W. N. Mathis, C. Feller (19 ♂, 25 ♀; USNM); South Water Cay, 1 Jun 1985, W. N. Mathis (2 ♂, 6 ♀; USNM).

Distribution.—United States (Florida: Lee Co., Sanibel Island), Belize, West Indies (Cuba, Dominica, and St. Vincent).

This the first record of *Paracanace* from the United States, although earlier, Mathis (1988:330) had included this genus in a key to the beach-fly genera from the United States with the expectation that the genus was likely to be found there. The new localities from the western Caribbean substantially increase the known distribution of this species, which previously was known only from Dominica in the Lesser Antilles.



Figs. 39–42. External male terminalia of *Paracanace aicen*: 39, Epandrium and surstylus (holotype from Dominica), lateral view; 40, Epandrium and surstyli (holotype from Dominica), posterior view; 41, Epandrium and surstylus (Florida, Lee Co., Sanibel Island), lateral view; 42, Epandrium and surstyli (Florida, Lee Co., Sanibel Island), posterior view.

The species may eventually be found to be circumcaribbean, but the paucity or absence of canacid collections from Colombia, Venezuela, and most countries of Central America precludes assessment of this possibility.

Natural history.—The specimens from Florida were collected on the causeway between the Gulf Coast of Florida and Sanibel Island (Lee Co.). The sides of the causeway, particularly the south side, were partially lined with broken pieces of concrete and large rocks to moderate the erosive action of waves. Much of the surface of the concrete and rocks was covered with algae. In addition to this species, beach flies of the following two species were also found in this habitat: *Procanace dianneae* (very abundant; see treatment below) and *Canacea macateei* (uncommon; see treatment above).

Although this species and *Nocticanace texensis* both occur on Carrie Bow Cay and are found in essentially the same habitats, I did not collect the two species together during a particular season. In the Lesser Antilles (Dominica and St. Vincent), I found the two species in the same sweep of the net, although in very unequal numbers. Where one species was common, the other was not. Whether this is an artifact of sampling or is indicative of temporal partitioning needs further investigation. Indeed, to what degree these two species may compete for the same or similar resources merits closer scrutiny.

See comments under the treatment of *N. texensis* for further information concerning Carrie Bow Cay and the specific habitat where this species occurs.

Remarks.—This species is closely related and similar to congeners of the *hoguei* group but can be distinguished from the latter by the following combination of characters: middle anaclinate genal seta about one-half length of seta on either side; spinelike setae along costal margin variable, short, not as long as width of 1st costal cell, or long (the holotype), length equal or slightly greater than width of 1st costal cell; general appearance setose but less so than in *P. hoguei*; surstylus of male terminalia as illustrated (Figs. 39–42). After study of several males from the new material collected in Belize, Cuba, Dominica, and Florida, I have noted some variation, although slight, in the shape of the surstylus. The range in variation is as illustrated (Figs. 39–42); the illustrations also facilitate identification of this species. Based on the sampling available, the shape of the ventral surstylar margin in the male from Florida, both lateral and posterior views (Figs. 41, 42), is more characteristic of the species than that of the holotype, which is from Dominica (Figs. 39, 40).

Paracanace lebam Mathis & Wirth
Figs. 43–44

Paracanace lebam Mathis & Wirth, 1978: 530.

Distribution.—Jamaica. Point Henderson.

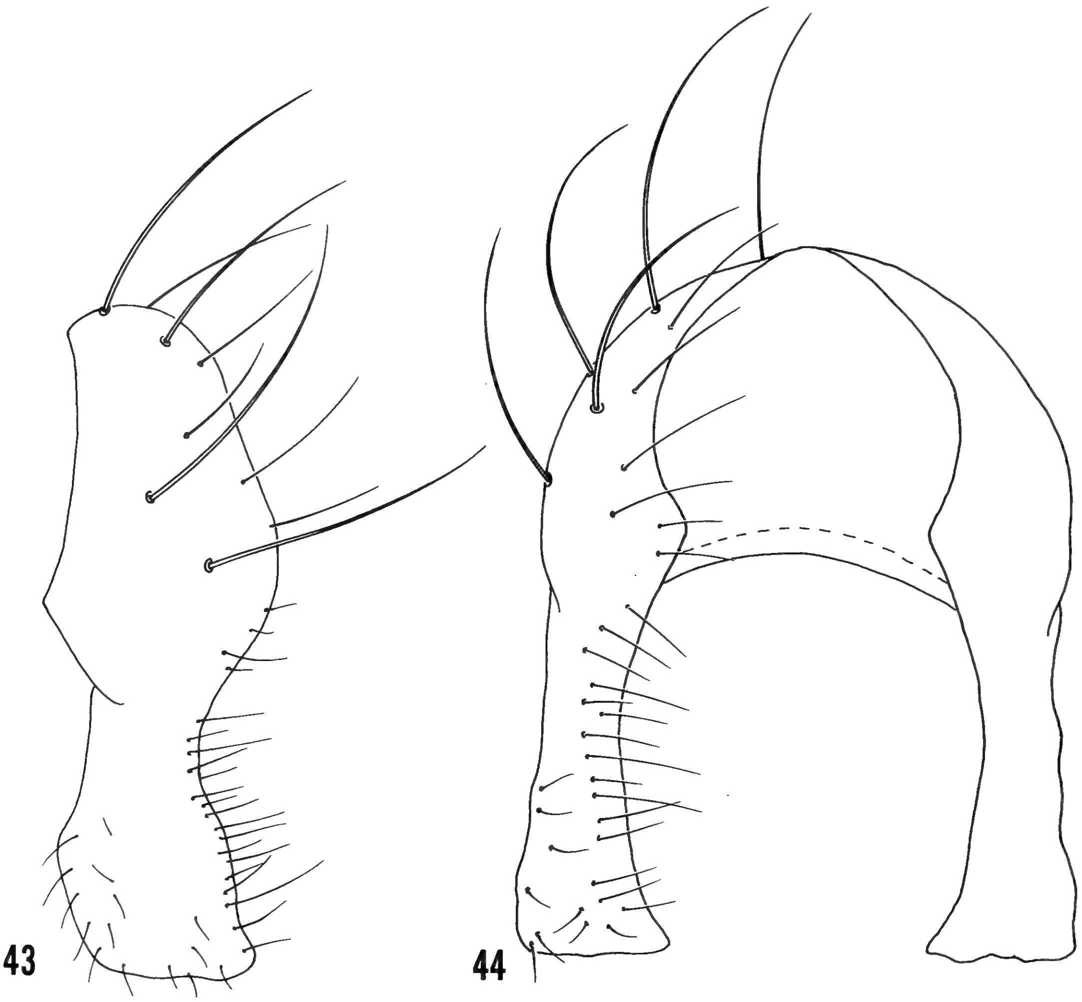
Remarks.—Externally, this species and *P. aicen* are very similar, but it may be distinguished from the latter by the following characters from the male terminalia: surstylus (Figs. 41, 42) broader on distal half, especially evident in lateral view; ventral margin of surstylus broadly truncate in lateral and posterior views; posterior margin of surstylus bearing distinct row of longer setae.

Genus *Procanace* Hendel

Procanace Hendel, 1913:93. Type species: *Procanace grisescens* Hendel, by original designation.—Mathis, 1988:329–333 [first record of genus from Western Hemisphere].

Diagnosis.—General coloration whitish gray, olivaceous, to blackish brown.

Head: Intrafrontal setae absent, but with a few setulae inserted anteriorly; fronto-orbital setae three; ocelli arranged to form equilateral or isosceles triangle, if isosceles,



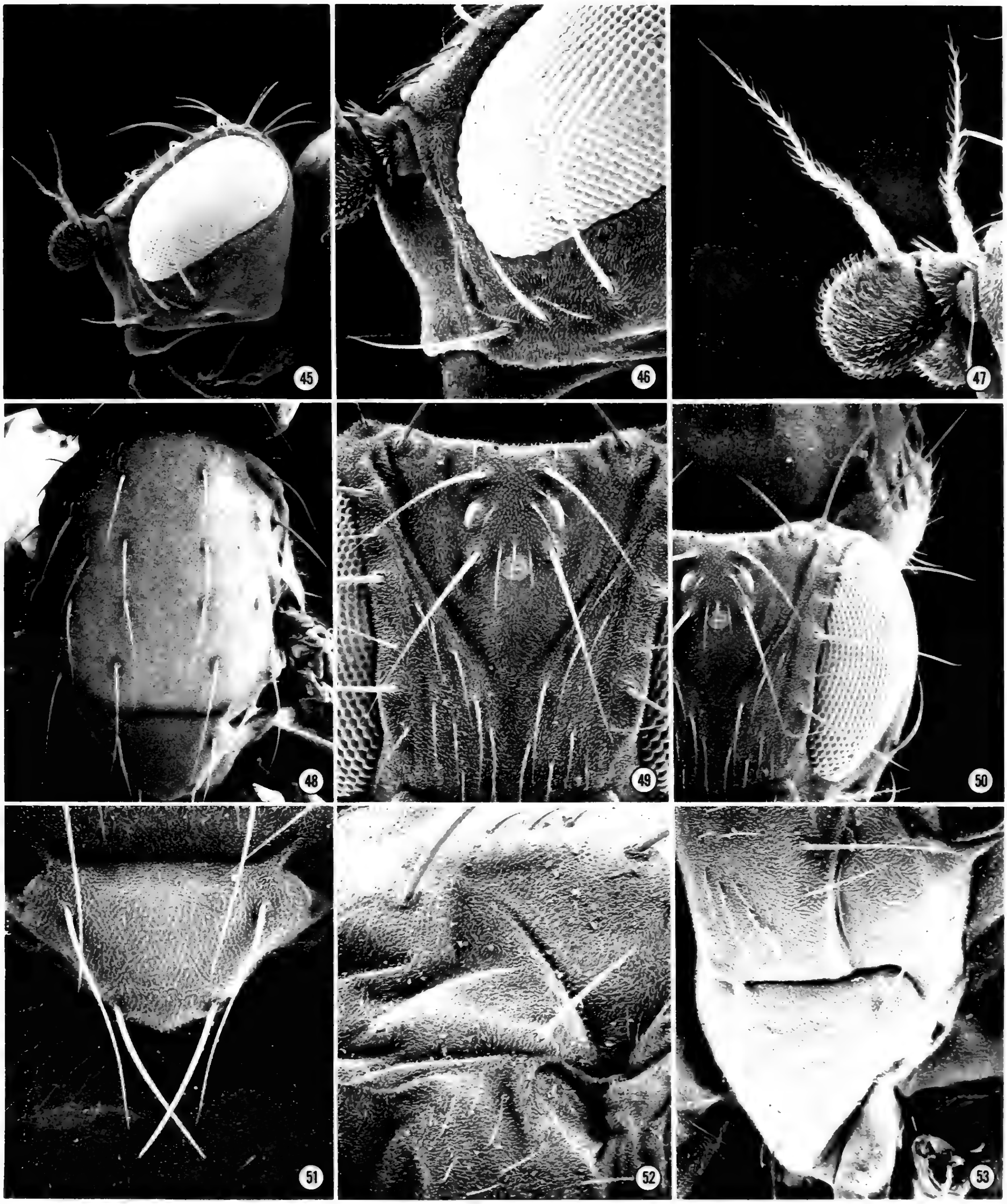
Figs. 43–44. External male terminalia of *Paracanace lebam*: 43, Epandrium and surstylus, lateral view; 44, Epandrium and surstyli, posterior view.

the greater distance is between posterior ocelli. Arista pubescent over entire length. Two large anaclinate genal setae; anteroclinate genal seta moderately well developed. Palpus not bearing long setae. Epistomal margin, in lateral view, more or less horizontal.

Thorax: Acrostichal setae, especially a prescutellar pair of large setae, usually lacking (setulae present in species of the *williamsi* group); scutellar disc lacking setae (one or two pairs of scutellar disc setulae occur in *P. nakazatoi* Miyagi of the *williamsi* group); two pairs of marginal scutellar setae, apical pair not anaclinate; anterior and posterior notopleural setae present, length of both subequal, anepisternum with scattered setulae. Katepisternal setae usually present (lacking in species of the *grisescens* group). Hind tibia lacking spine-like setae apically.

Abdomen: Male genitalia as follows: Epandrium in posterior view wider than high; cerci reduced, poorly sclerotized; surstylus with an anterior and posterior lobe, the latter larger, sometimes markedly so and shape unique to species.

Discussion.—Mathis (1988) first reported the occurrence of *Procanace* in the Western Hemisphere from specimens collected in Virginia along the tidal shores of the Potomac River. The species, *P. dianneae,* was then only known from Virginia, but recent collecting in North and South Carolina, as well as the Gulf Coast of Florida has resulted in discovery of this species along much of the eastern coast of the United States.



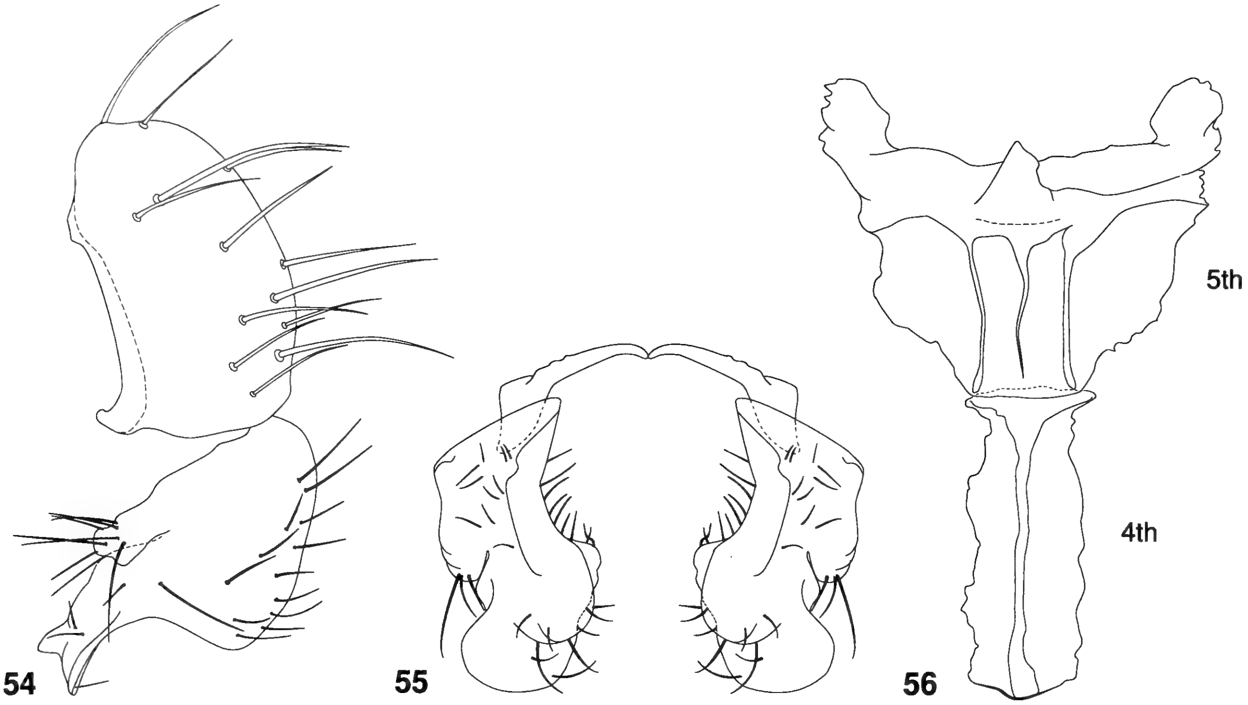
Figs. 45–53. Scanning electron micrographs of *Procanace dianneae*: 45, Head, lateral view; 46, Gena and setae, lateral view; 47, Antenna, lateral view; 48, Mesonotum, dorsal view; 49, Frons and ocellar triangle, dorsal view; 50, Fronto-orbital and vertical setae, dorsal view; 51, Scutellum, dorsal view; 52, Notopleuron and setae, lateral view; 53, Katepisternum and setae, lateral view.

Annotated Key to Species Groups of *Procanace* Hendel

1. Katepisternal seta absent .... the *grisescens* group [four species; Oriental, eastern Palaearctic, Oceanian, Malagasy, Seychelles]

– Katepisternal seta present 2

2. Clypeus high, width about twice the height; palpus blackish brown;



Figs. 54–56. External male terminalia of *Procanace dianneae*: 54, Epandrium and surstylus, lateral view; 55, Surstyli, posterior view; 56, Fourth and fifth sterna, ventral view.

proepisternal seta absent .... the *nigroviridis* group [seven species; Hawaiian Islands]
– Clypeus low, width at least four times the height; palpus yellowish; proepisternal seta(e) present 3
3. Acrostichal setulae present, in two irregular rows .... the *williamsi* group [four species; Hawaiian and Ryukyu Islands]
– Acrostichal setulae absent 4
4. Postocellar setae either absent or much reduced .... the *fulva* group [nine species; Oriental and eastern Palaearctic]
– Postocellar setae present, subequal to length of ocellar seta .... the *cressoni* group [three species; Oriental, Nearctic]

Procanace dianneae Mathis
Figs. 45, 46

Procanace dianneae Mathis, 1988:330–333.

Distribution.—Eastern coast of the United States from Virginia south through North and South Carolina to Florida, including the Gulf Coast.

Natural history.—The type series was taken along the tidal shore of the Potomac River where the water is only slightly brackish. The additional distribution sites reported here are oceanic (Atlantic and Gulf of Mexico), with distinctly saline water. On Kure Beach (North Carolina, Brunswick Co.), the specimens were extremely abundant on the sandy shore within a protected area where boats could be launched. The exposed sand was largely covered with algae that had washed ashore. At Cherry Grove (South Carolina, Horry Co.), the specimens were found exclusively on the concrete foundations of a fishing pier. The foundations nearest the shore are exposed at low tide and most high tides and were partially covered with algae. A species of *Tethina* (probably *albula* (Loew); Tethinidae) and *Fucellia* (Anthomyiidae) also occurred on the foundations. The causeway leading to Sanibel Island (Gulf Coast side of Florida, Lee Co.) had portions of the shore that were lined with large chunks of concrete and rock to brake the erosive action of waves, and the specimens *P. dianneae* mostly occurred where the wave action was dampened by the rocks and concrete that were also extensively covered by algae. Two other beach flies, *Canacea macateei* and *Paracanace aicen,* also occurred on the causeway.

Remarks.—Externally this species is very similar to those of the *cressoni* group. It differs from the two species of that group, *P. cressoni* Wirth and *P. taiwanensis* Delfinado, as well as other congeners by the following combination of characters: Postocellar setae well developed, subequal in length to ocellar setae; clypeus low, height one-fourth width; palpus yellowish. Scutum mostly bluish black, sparsely microtomentose, scutum densely microtomentose, brown; proepisternal seta present, pale; katepisternal seta present; acrostichal setae absent. Shape of the male genitalia unique (see figs. and description above).

As noted previously, this species was only recently discovered in Virginia, and it has now been found to occur along the East Coast of the United States from Virginia to Florida, including the Gulf Coast. Apparently the species either dispersed rapidly along the East Coast after its introduction, perhaps similar to *Brachydeutera longipes* Hendel (Mathis and Steiner 1986; Ephydridae), or it has resided here for some time without being detected.

Acknowledgments

I am grateful for the assistance in the field from Jorge L. Fontenla (IZAC) and the other collectors as noted in the text. For the loan of the holotype of *Canaceoides texensis,* I thank Paul H. Arnaud, Jr. (CAS). For critically reviewing a draft of this paper, I thank Amnon Freidberg, Oliver S. Flint, Jr., and I. Candida Feller. The pen and ink illustrations were skillfully inked by George L. Venable, and Susann Braden provided technical support for the scanning electron micrographs. Funding for this research project was provided in part by the American Philosophical Society (grant number 9284, Penrose Fund) and a grant from the Research Opportunity Fund (Smithsonian Institution). Their support is gratefully acknowledged.

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A SMALL COLLECTION OF HETEROPTERA FROM THE GALAPAGOS ISLANDS, WITH THE DESCRIPTION OF THE NEW SPECIES *NIESTHREA ASHLOCKI* AND A LIST OF *NIESTHREA* SPECIES (RHOPALIDAE)

Richard C. Froeschner

Abstract.—Report on seven species of Heteroptera from the Galapagos Islands: Five confirm reported occurrences on Santa Cruz Island; one new island record of *Harmostes disjunctus* Barber from Fernandina Island; and description of one new species, *Niesthrea ashlocki* taken from *Sida acuta* Burmann [Malvaceae] on Santa Cruz Island, most closely allied to the Brazilian *N. digna* Chopra. Description of the new species accompanied by dorsal habitus drawing and sketch of male genital capsule. Included is a checklist of the species of *Niesthrea* Spinola.

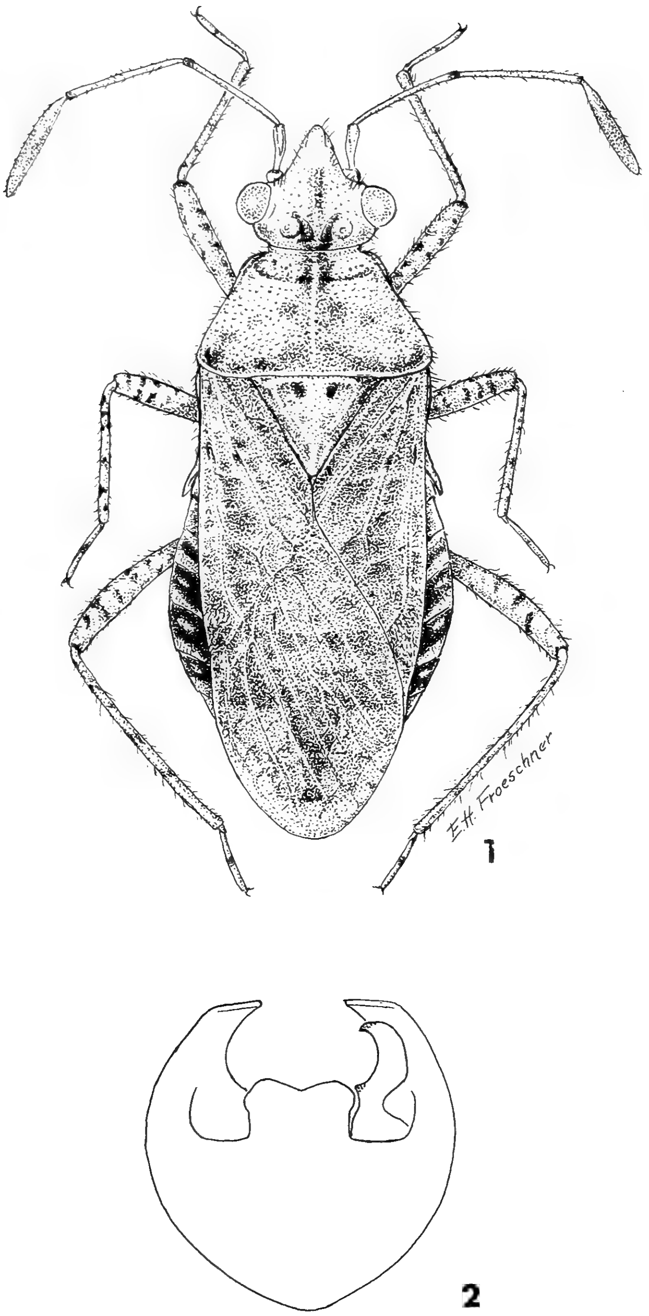
Subsequent to the appearance of my synopsis of the Heteroptera of the Galapagos Islands (1985) Dr. Peter D. Ashlock (University of Kansas, Lawrence) submitted for my study a small collection of Heteroptera he made on the Galapagos Islands during the period of January to May of 1964. All specimens but one were from Santa Cruz Island and included the following: Berytidae: *Metacanthus galapagoensis* (Barber) [in abandoned garden]; Coreidae: *Anasa obscura* Dallas [from "*Mamortlca*" (probably a misspelling for the Cucurbitaceae genus *Momordica*) *indica*; in abandoned garden]; Miridae: *Horcias lacteiclavus* Distant [part of the population discussed by Carvalho (1968:200); Pentatomidae: *Acrosternum viridans* (Stal) [at light; in abandoned garden]; *Podisus sordidus* (Stal) [from *Psidium* sp.]; Rhopalidae: *Harmostes disjunctus* Barber, including nymphs; *Niesthrea ashlocki*, new species described below [from *Sida acuta* Burmann]. One new island record was included based on a broken specimen of *Harmostes disjunctus* taken in the Miconia Belt at 1300–2100′ on the SW side of Fernandina Island, 4 Feb 1964, P. D. Ashlock.

The New World genus *Niesthrea* Spinola (1837:245), in the tribe Niesthrini, was not previously reported for the Galapagos Islands. In my (1985) synopsis it would key to *Liorhyssus* in couplet 2 on page 49. *Niesthrea*'s pronotum lacks the subapical, calloused, impunctate, transverse ridge that is characteristic of *Liorhyssus*. Chopra (1973) presented a revision of the genus *Niesthrea* based principally on male genitalic characters.

Niesthrea ashlocki, new species
Figs. 1–2

Diagnosis.—Males are easily recognized to species by the shape of the medioventral lobe on the genital capsule plus the length of the claspers (Fig. 2): Medioventral lobe broad, lateral expansion subangularly convex; exposed part of clasper gently curved, apically more strongly incurved to a subacute tip, exposed part of clasper elongate, extending by half its length beyond apex of medioventral lobe.

Description (measurements in millimeters).—Holotype male, length 5.35; general



Figs. 1–2. *Niesthrea ashlocki*, new species: 1, dorsal view; natural length 5.3 mm; 2, male genital capsule, ventral view, left clasper omitted.

color yellowish; head clouded with fuscous on midline between eyes, with a pair of diverging, deep-black lines between ocelli. Antenna yellow, segment I mesally and laterally with an oblique, fuscous line; segments II and III with a blackened line extending almost full length, II blackened apically. Pronotum with median fuscous area divided by pale median carina; posterior lobe with humeri, subbasal margin, and diagonal row of a few fuscous spots. Scutellum with subbasal pair of brown spots. Hemelytral veins with a few reddish-brown dots. Dorsal disc of abdomen (viewed through hyaline hemelytra) mostly black; connexival segments apically pale, visible segments III–V basally broadly black, each with an included pale dot, the black extending onto margin of venter. Legs yellow, appearing annulate due to transverse dark marking extending more or less around femur and tibia.

Head.—Length 0.90, width across eyes 1.15; preocular part convex, tylus distinctly produced anteriorly; antennal tubercles short, apex transverse. Antennal, segment lengths I–IV, 0.36:0.87:0.87:0.95, segment I reaching apex of tylus. Labium reaching basal segment of abdomen, lengths of segments I–IV, 0.53:0.71:0.53:0.76, segment I reaching hind margin of eye.

Pronotum, length 0.90, width 1.77.

Genital capsule (Fig. 2) with medioventral lobe broader than long, constricted basally, apical margin subangularly concave, laterally subangularly convex; dorsolateral lobe (best viewed from above) distinctly incurved, markedly surpassing apex of medioventral lobe. Exposed part of clasper gently curved, apex projecting mesally as an acute tip, inner margin near apex of capsule with a small tooth.

Female.—Length 5.58. General appearance similar to male but more abundantly dotted on pronotum; ventrally with red dots on thoracic pleurae. Last abdominal tergum rounded. Last abdominal sternum not notched. Head, length 1.15, width 1.23. Antennal segment lengths, I–IV 0.37:1.50:1.50:1.20. Labial segment lengths, I–IV, 0.57:0.76:0.62:0.82. Pronotum, length 1.25, width 2.06.

Holotype male.—"Galapagos, 4 mi. [6.4 km] N Academy Bay, Santa Cruz Is., 21 Feb 1965, P. D. Ashlock, *Sida acuta* Burm. [Malvaceae]." Paratype: one female, Galapagos Arch.[ipelago], Santa Cruz Is., 2.4 km N Academy Bay, 25 Feb 1964, P. D. Ashlock. Holotype and lone paratype in the National Museum of Natural History.

Placement of this new species in the phylogeny (based solely on males) proposed by Chopra (1973) in his revision of the genus *Niesthrea* may be made as follows. Three modifications of the male genital structures (Fig. 2) place it on the same branch of Chopra's (1973:457) "Phylogenetic tree" with *N. digna* Chopra: genital capsule with dorsolateral lobes incurved apically, medioventral lobe broader than long, and clasper apically incurved to form an acute angle. It differs from *N. digna* in having both the dorsolateral lobes and the clasper greatly surpassing the apex of the medioventral lobe, the claspers by almost half their own length and the dorsolateral lobe extending beyond them. The Galapagos Islands occurrence of *N. ashlocki* is geographically remote from the Brazilian homeland of *N. digna.*

The species name is a dedication to Dr. Peter D. Ashlock, the collector whose many contributions to heteropterology have soundly advanced that science.

Checklist of the Species of *Niesthrea* Spinola

The following list is an expanded version of that given on pages 52–56 of Göllner-Scheiding's (1983) catalog of the family Rhopalidae.

agnes Chopra, 1973:455	Argentina
ashlocki, new species	Galapagos Islands
brevicauda Chopra, 1973:455	Peru
dentata Chopra, 1973:454	Brazil
digna Chopra, 1973:453	Brazil
fenestrata (Signoret), 1859:93	Chile
flava Grillo & Alayo, 1978:43	Cuba
louisianica Sailer, 1961:297	U.S.A.; Mexico
parasidae Grillo & Alayo, 1978:46	Cuba
pictipes (Stal), 1859:239	Argentina; Brazil; Paraguay
subsp. *pictipes* (Stal), see species entry	
subsp. *casinii* Göllner-Scheiding, 1984:116	Argentina; Uruguay
sidae (Fabricius), 1794:169	Greater and Lesser Antilles; Colombia; Mexico; United States; Venezuela
similis Chopra, 1973:453	Argentina; Brazil
ventralis (Signoret), 1859:89	Guatemala; Mexico; United States
vincentii (Westwood), 1842:6 and 26	Greater and Lesser Antilles; Argentina; Brazil; Paraguay; Venezuela

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My appreciation is expressed to Dr. John J. Wurdack, Smithsonian Institution Department of Botany, for his help in deciphering the misspelled host genus for *Anasa obscura*; to Ms. Silver B. West for help in preparing the manuscript; to Ms. Elsie Froeschner for the drawings, and to Dr. Oliver S. Flint and Mr. Thomas J. Henry for helpful reviews of the manuscript.

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Stal, C. 1859. Hemiptera: Species novas descripsit. Kongliga Svenska Fregattens Eugenies Resa Omkring Jorden, III (Zoologi, Insekter). Pp. 219–298, pls. 3–4.

Westwood, J. O. 1842. A catalogue of Hemiptera in the collection of the Rev. F. W. Hope, with short Latin descriptions of the new species. 2:1–26.

Note: The honoree of the new species, Dr. Peter D. Ashlock, died 26 January 1989.

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CANCER JOHNGARTHI, N. SP. AND *CANCER PORTERI* (BELL) (CRUSTACEA, DECAPODA): COMPARISONS AND HYPOTHESIS

Alberto Carvacho

Abstract.—*Cancer johngarthi,* long mistaken for *C. porteri,* is described. It is known in the eastern Pacific from Isla Guadalupe, Mexico (29°N), south to Panama (7°N), on soft bottoms at depths exceeding 90 m. Differences from *C. porteri* are discussed with an emphasis on biological aspects: *C. johngarthi* shows an isometric growth of chelipeds in relation to carapace width, while in *C. porteri* a strong positive allometry is evident after the puberal molt. These two conditions may reflect different mating systems.

The species *Cancer porteri,* described by Bell (1835) as *C. longipes,* was transferred to the genus *Platycarcinus,* synonym of *Cancer,* by H. Milne-Edwards & Lucas (1844), and given its present name by Rathbun (1930). Nations (1975) included it in the subgenus *Cancer* s.s. The holotype was collected in Valparaíso, Chile. Faxon (1895) recorded it from Panama Bay as deep as 523 m (*Albatross*). These two eastern Pacific localities, 33°S and 7°30′N, respectively, were long considered as the geographic distributional limits of the species.

Garth (1957) cited a continuous distribution "from Callao, Peru to Valparaiso, Chile, 0–24 fms" and an extralimital record from Panama. Nevertheless, he also included in the list of examined material one male collected by the Lund University Chile Expedition at Talcahuano (36°41′S), some 450 km south of Valparaíso. This latter record has been confirmed by Retamal & Yáñez (1973). Garth (1961) recorded *C. porteri* from the coast of Sinaloa in the Gulf of California, between 108 and 128 m, and mentioned that the species "may now be reported as a bi-temperate species that transgresses the tropics by submergence, being found in the Gulf of California, the Bay of Panama in 210 to 286 fathoms, and from Peru to Chile in the Sublittoral."

Information gathered during almost 150 years supported the idea that *C. porteri* was a eurybathic species with a wide geographic distribution. In fact, the case has been used as a paradigm of the peculiar tropical submergence distribution pattern (Ekman 1953, Garth 1961).

Careful study of several specimens recently collected off Baja California Sur and the reexamination of virtually all specimens identified with *Cancer porteri* from the Northern Hemisphere, along with several specimens from Chile and Peru, leads to the conclusion that they belong to two different species. The morphological differences, scarcely evident in young specimens, may express divergence in their mating systems.

Cancer johngarthi, new species
Figs. 1, 3A, 4B

Cancer longipes, Faxon, 1895:16; Rathbun, 1930:199 (in part).

Cancer porteri Rathbun, 1930:199 (in part); Garth, 1957:50 (in part); 1961:122; Parker, 1964:173; Chirichigno, 1970:45 (in part); Retamal & Yáñez, 1973:12 (in part);

Nations, 1975:43 (in part); 1979:154, 156, 178 (in part); Retamal, 1981:30 (in part).

Carapace granulated, widely oval, very convex and moderately areolated, with protuberances on proto- and mesogastric regions and on borders of epi- and mesobranchial regions. Both mesobranchial regions swollen and nearly meeting in median line. Frontal region convex. Front projected and furnished with 3 teeth, median slightly longer and narrower than others. Inner orbital tooth pointed and slightly shorter than frontal teeth. Anterolateral margin finely granulated, cut into 9 teeth; granulations enhanced posteriorly. Posterolateral margin granulated and furnished with 2 teeth, first small and second vestigial, sometimes imperceptible. Pterygostomial region swollen and coarsely granulated towards outer edge. Whole carapace remarkably thin; epi- and subbranchial and pterygostomial regions may be easily flexed.

Buccal cavity well delimited anteriorly by projections of pterygostomial border, with 2 strong vaults separated by a longitudinal keel.

Maxillipeds granulated, with ischium and merus widened distally. Merus with outer face concave and a notch on distal half of inner margin where palp inserts.

Chelipeds: fingers with tips and cutting edges dark, starting from proximal tooth. Palm granulated, with 4 longitudinal carinae on lower half of outer face. Propodus 2.7 times as long as wide in adult males. Carpus rough, with irregular granulated carinae and anterosuperior pyramidal tooth. Merus with subtriangular section and upper distal margin granulated.

Walking legs long and slender, without spines or setae on proximal articles. Propodus with scarce setae on distal end of lower margin. Dactylus with 4 symmetrical longitudinal rows of setae and a deep groove along inner and outer faces, respectively.

Abdomen in adult males with terminal segment narrowly rounded distally, lateral margins slightly concave and 1.1 times as long as wide. Adult males with second pleopod slightly overreaching second segment of thorax; first pleopod slightly overreaching third segment of thorax.

Holotype.—In the collection of the Allan Hancock Foundation: male (carapace 14 cm wide, 8.7 cm long); Isla Guadalupe, Mexico; 183 m; 15 Nov 1968, *Velero IV* sta. 12460–68; catalog number AHF 6815.

Material examined.—Paratypes: Isla Guadalupe, Mexico (29°N); 183 m, 15 Nov 1968, *Velero IV* sta. 12460–68; 4 males, 1 female, AHF 6816. Off Río San Lorenzo, Sinaloa, Mexico (24°15′N), 108–128 m; May 1959; 2 males, 6 females; AHF 5929. Off Bahía Magdalena, B.C., Mexico (24°15′N), 90–125 m; Jul 1987, 1 male, 3 females, CIB, La Paz. Bahía de Panama; 384 m; Mar 1891; *Albatross* sta. 3389; 1 female, MCZ, Harvard University.

Distribution.—Eastern Pacific from Isla Guadalupe, Mexico to Bahía de Panama. Southern Gulf of California.

Habitat.—Soft bottoms, 90–523 m.

Etymology.—Named in honor of Dr. John S. Garth, Chief Curator Emeritus, Allan Hancock Foundation, University of Southern California, Los Angeles, California.

Comparison with *Cancer porteri*

The observations listed below and also data for Figs. 3 and 4 resulted from the examination of 17 specimens of *C. johngarthi* (carapace widths from 35 to 140 mm) and 43 specimens of *C. porteri* (c.w. 22.8 to 123 mm). These latter came from Valparaíso, Chile and from the following localities in Peru: Bahía Independencia, Bahía San Juan, Isla San Lorenzo, Bahía San Nicolás, Callao, Isla Lobos de Afuera.

1. Chelipeds of adult males noticeably stronger in *C. porteri* (Fig. 2a). As shown in Fig. 3B this allometric character is better expressed after the molt of puberty.

2. Darkening in cutting edges of cheliped fingers starts proximally in *C. porteri* but in *C. johngarthi* it starts at first tooth.

3. The most remarkable difference at any

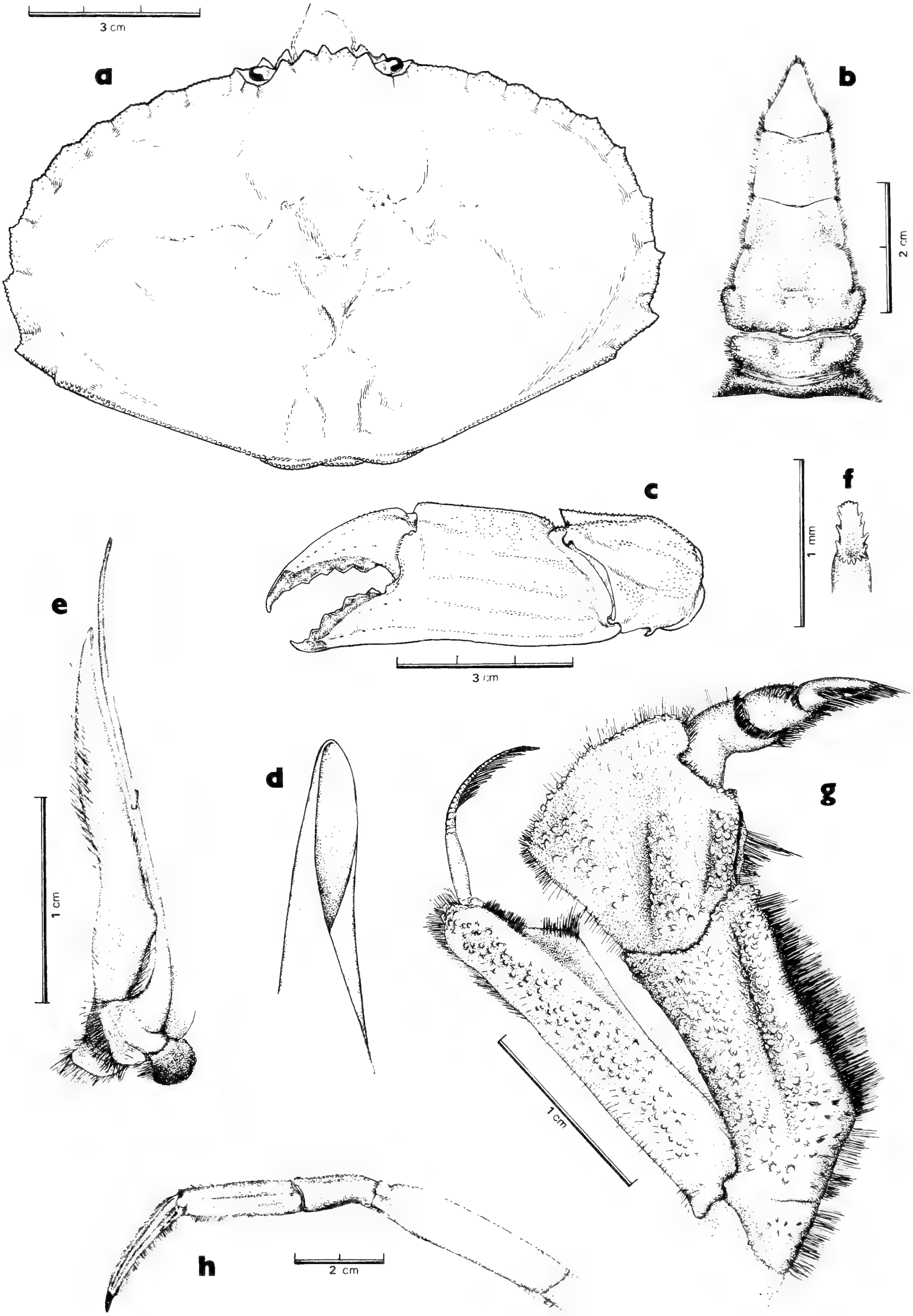

Fig. 1. *Cancer johngarthi*, male: a, Carapace, dorsal; b, Abdomen; c, Left cheliped; d, Second pleopod, distal end; e, First and second pleopods; f, First pleopod, distal end; g, Third maxilliped.

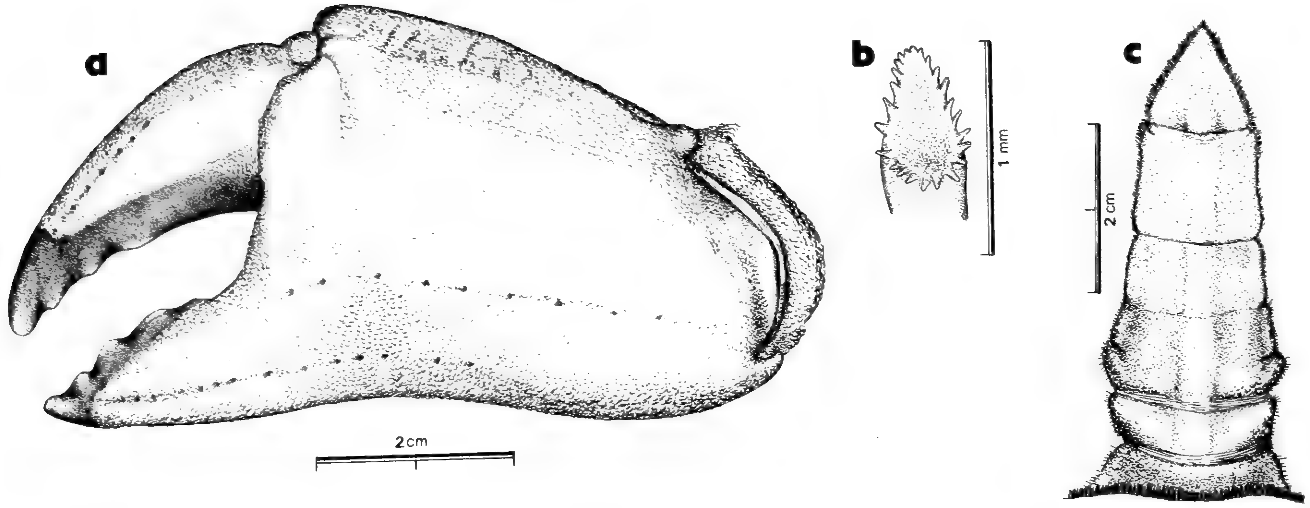

Fig. 2. *Cancer porteri*, male: a, Left cheliped; b, First pleopod, distal end; c, Abdomen.

age is consistency of the carapace. *C. johngarthi* seems to be a paper shell species.

4. Terminal segment in abdomen of males with straight lateral margins in *C. porteri* and slightly concave margins in *C. johngarthi* (Figs. 1b and 2c).

5. Pereopods proportionately longer and dactyli of walking legs longer in relation to propodi in *C. johngarthi.*

6. Width/length relation of carapace significantly greater in *C. johngarthi* (Fig. 4).

7. As shown in Figs. 1f and 2b, apex of first male pleopods quite different in each species.

Habitat preferences of each species are not sufficiently documented, but *C. johngarthi* seems to prefer deeper waters; it has not been collected shallower than 90 m while *C. porteri* inhabits waters from the intertidal to more than 350 m (Yáñez 1974). This scheme agrees with the well known relation of *Cancer* and water temperature: species in this genus usually live at latitudes greater than those where the surface isotherm of 20°C is to be found (MacKay 1943, Nations 1979). At lower latitudes depth compensates thermal needs; such is the case of *C. borealis* and *C. irroratus* in Florida, and especially *C. guezei* in Madagascar (Crosnier 1976).

The Hypothesis

The genus *Cancer* originated in the northeastern Pacific (Ekman 1953, Nations 1975, 1979) and dispersed southward along the west coast of the Americas. Four species may be found in Peru and Chile; one of these is *C. porteri.* This species, now separated from *C. johngarthi,* ranges from Isla Lobos de Afuera (6°57′S) to Talcahuano (36°41′S), covering most of the Peruvian-Chilean province (sensu Briggs 1974). The morphological affinity and geographic distribution of the two species suggest the existence of a common ancestor that traveled—perhaps in the Miocene—between North and South America (Nations 1979).

Morphological divergence between *C. johngarthi* and *C. porteri* may have resulted from different mating systems. Orensanz & Gallucci (1988) explain some differences among four sympatric species of *Cancer,* such as dimorphic development of chelipeds, according to the models of polygyny established by Emlen & Oring (1977). Mating systems of species with precocious development of a strong cheliped may be interpreted as a case of resource defense polygyny: in *C. oregonensis* each male holds a refuge area—limited resource—which al-

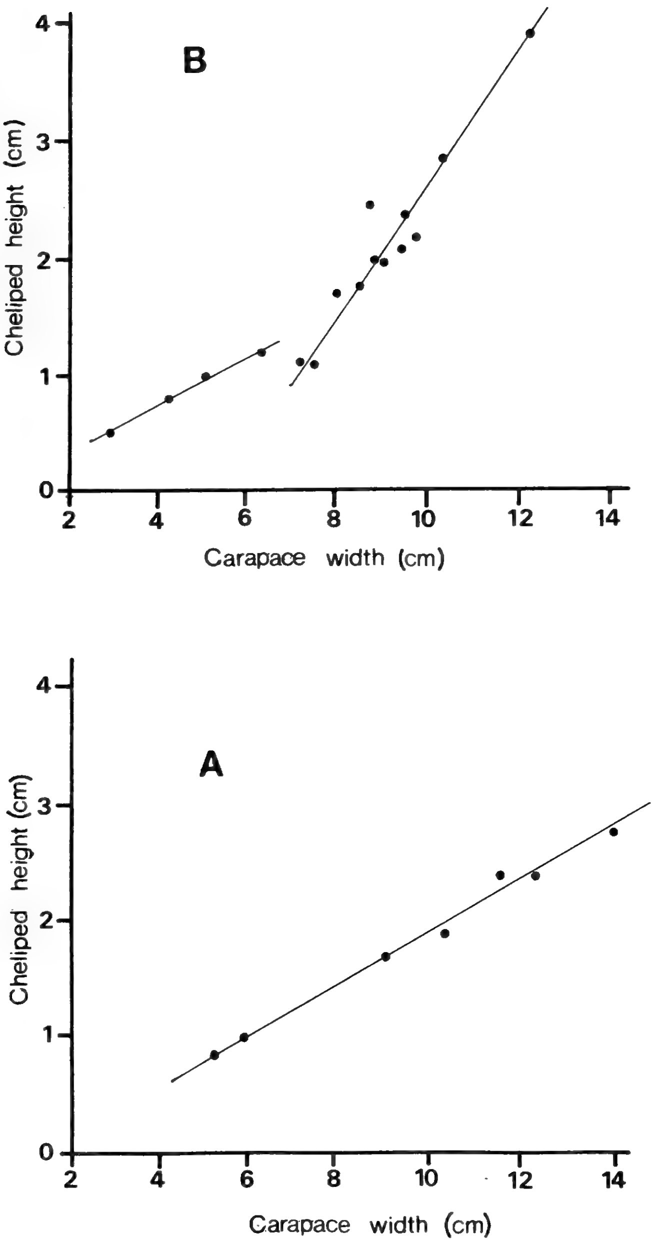

Fig. 3. Cheliped height plotted against carapace width in males: A, *Cancer johngarthi*; B, *Cancer porteri.*

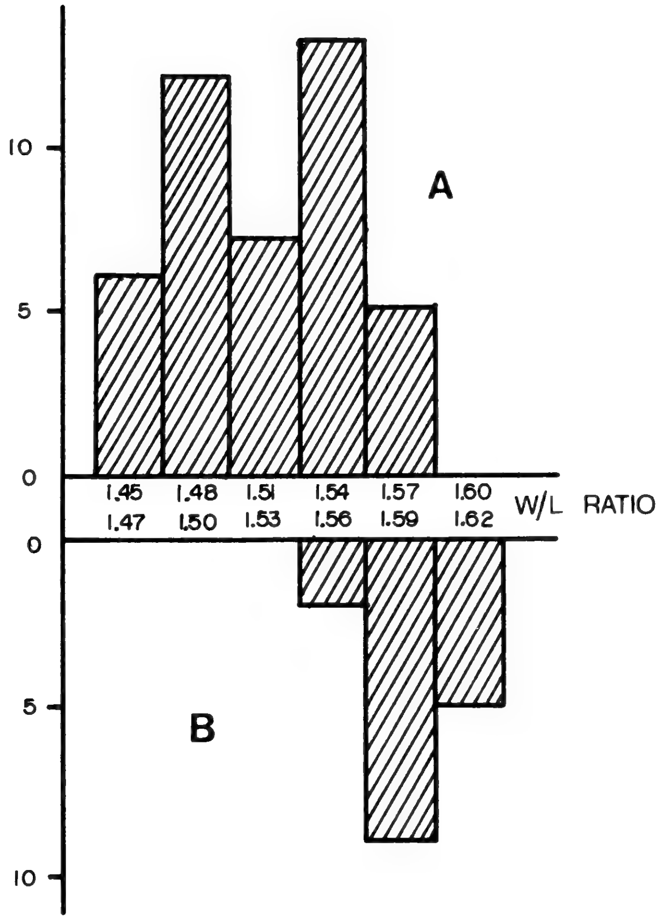

Fig. 4. Frequencies of width to length ratios in carapaces: A, *C. porteri*; B, *C. johngarthi.*

lows him to monopolize females. Precocious development of strong chelipeds is required for an early appropriation of adequate refuges. The case of harem defense polygyny involves direct access to females; therefore, defense strategies are only needed once reproductive size is reached. Positive allometric growth of chelipeds, consequently, starts just after the molt of puberty. This seems to be the case for *C. porteri*, as indicated by allometric growth of male chelipeds (Fig. 3B) and also by data in Antezana et al. (1965) who determined a figure of 5 females per each male after one year of monthly sampling.

In the third model, male dominance polygyny, mates or critical resources are not economically monopolizable. Males aggregate during the breeding season and females select males from these aggregations. Sexual dimorphism in the development of chelipeds is not expected here. Orensanz & Gallucci (1988) included *C. magister* in this category, stressing the fact that *C. magister* is the only species in the genus *Cancer* in which chelipeds are of the same size in males and females. I suggest that this is also the case for *C. johngarthi*, in absence of dimorphic development of chelipeds. Several additional arguments uphold this hypothesis. As expected, sex ratio is almost 1:1 and sexual selection nearly null; from a total of

27 known specimens of *C. johngarthi*, 15 are males and the rest females. Since breeding assemblages are not permanent, breeding season should be normally restricted to a short period of time; this seems a reasonable explanation for the lack of ovigerous females in the collected material.

On the other hand, there is a relation between size of cheliped and quality of substrate. Species inhabiting soft and homogenous bottoms of fine sand have chelipeds proportionately weaker than those from irregular rocky substrates. Lawton & Elner (1985) stated that these differences account basically for the type of feeding, but they left aside an important element of analysis, the role of chelipeds in sexual selection, which is common to most decapod Crustacea. Evidently, differences in size and shape of chelipeds of dimorphic species are not due to differences in diet of each sex; male chelipeds fulfill other functions such as the defense of a territory or of a harem. Sudden development of cheliped dimorphism at molt of puberty in many species is strong evidence of cheliped morphology depending primarily upon sex requirements. Open soft-bottom environments, compared to complex rocky substrates, allow fewer possibilities of delimitation and defense of a territory; therefore, different mating systems are involved. Following this idea, lack of dimorphism in chelipeds of *C. johngarthi* may be interpreted as a consequence of a male dominance polygyny mating system that in turn results from inhabiting open soft bottoms.

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STENORHYNCHUS YANGI, A NEW WESTERN ATLANTIC SPECIES OF ARROW CRAB (CRUSTACEA, BRACHYURA, MAJIDAE) AND A REDESCRIPTION OF *S. SETICORNIS* (HERBST, 1788)

Gary D. Goeke

Abstract.—The common arrow crab of the western Atlantic has a complicated taxonomic history as two species have long been confused under the name *Stenorhynchus seticornis* (Herbst, 1788). Through study of living specimens and preserved material in museums of North and South America, as well as Europe, the genus *Stenorhynchus* Lamarck, 1818, is reviewed, *S. seticornis* is restricted, its synonyms discussed, and a previously undescribed species, *S. yangi*, is recognized. Adults of these two species are described and illustrated, their morphologic variations analyzed, colors differentiated, known geographic and bathymetric ranges recorded, and their larvae compared. The species differ in rostral setation, shape of male first pleopod, and in other characters. Moreover, two ecophenotypes related to substrate can be recognized within *S. seticornis*.

The common shallow-water arrow crab, *Stenorhynchus seticornis* (Herbst, 1788), of the western North Atlantic is such an obvious component of the marine fauna that it has been described under several different scientific names over the past 200 years. It has become evident through the work of Yang (1967, 1976) on larval development in majids and on taxonomic problems in the genus *Stenorhynchus* Lamarck, 1818, that two species are confused under the name *Stenorhynchus seticornis* (Herbst, 1788) (Fig. 1).

Historical Review

The group of spider crabs currently assigned the generic name *Stenorhynchus* has a wide distribution in warm and temperate waters of the Atlantic and eastern Pacific oceans. Species now grouped within this genus were previously assigned to various genera until taxonomic consistency was reached with the use of the generic name *Leptopodia* Leach, 1814. Arrow crabs are very common and led Milne-Edwards (1875: 173) to state, "Cette espèce est si bien connue, et elle a été si souvent figurée, qu'il est inutile d'en donner ici une description." *Leptopodia* is now known to be a junior synonym of *Inachus* Weber, 1795, and not a valid generic name for this group. *Cancer sagittarius* Fabricius, 1793 (=*Stenorhynchus seticornis*) was transferred to the genus *Leptopodia* by Leach in 1815 and was considered the type for the genus. However, *Leptopodia* was erected for *Cancer phalangium* Pennant, 1777, and *Leptopodia tenuirostris* Leach, 1814. Because *Cancer sagittarius* was not mentioned in the original description of *Leptopodia*, it could not serve as the type species. Lamarck (1818) erected the genus *Stenorhynchus* for *Cancer seticornis* Herbst, 1788, and *Cancer phalangium*. The latter species, however, is a member of the genus *Inachus*. Since the des-

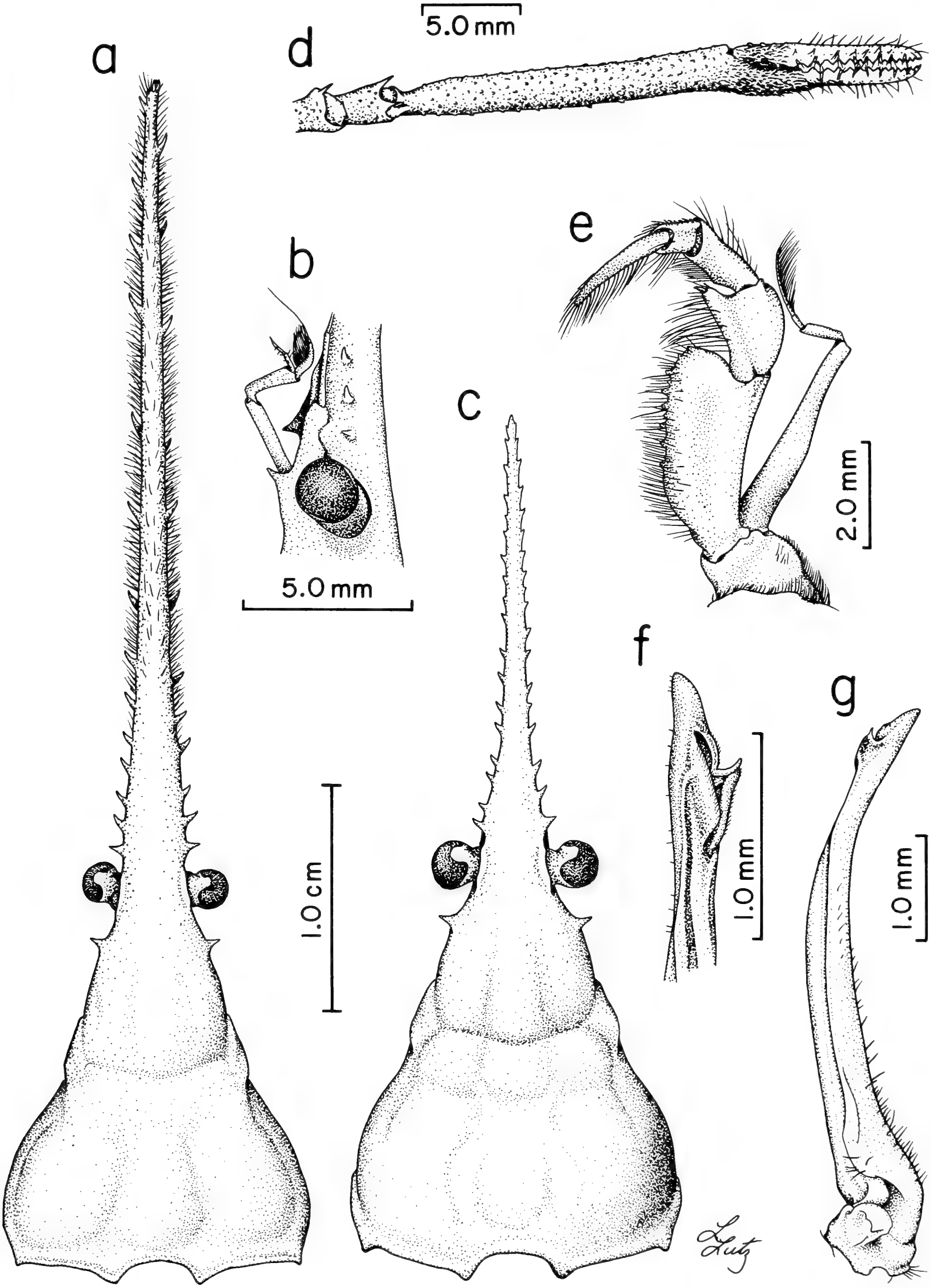

Fig. 1. *Stenorhynchus seticornis*, a, b, d, e, f, and g; *Stenorhynchus yangi*, c.

ignation of the name *Stenorhynchus* by Rathbun (1897) as an available name for the group, it has been widely accepted. Garth & Holthuis (1963) petitioned the International Commission on Zoological Nomenclature (ICZN) to designate *Cancer seticornis* Herbst, 1788, the type species of the genus and to officially emend the spelling of the generic name from *Stenorynchus* to *Stenorhynchus*. These recommendations were followed in opinion 763 of the ICZN.

Five binomials may bear on western Atlantic species of *Stenorhynchus*, the earliest of which is the description of the "Oost-Indische Zee-Krabbe" by Slabber (1778). This "East Indies Sea Crab" was described in very general terms which dealt primarily with the gross morphology of the carapace and legs. The specimen, a female from the description of the abdomen, was characterized as having small setae on the sides of the rostrum. The very generalized illustration accompanying Slabber's (1778: pl. 18, fig. 2) description includes a single useful morphologic feature for specific taxonomic purposes, and even that is of limited diagnostic value for taxa within this group. The figure indicates a rostrum twice the length of the postorbital region of the body. However, the drawing of the original figure is questionable because the crab is not accurately depicted, as evidenced by the lack of spination on the ambulatory legs. Although no doubt exists as to the genus with which Slabber dealt, the morphological characters considered useful for specific identifications by today's standards were not detailed by that author.

The type locality of the "East Indies Sea Crab" as given by Slabber is incorrect. Holthuis (1959:185) noted that the genus *Stenorhynchus* is not represented in the Indo-West Pacific and that material from which the description was drawn was apparently mislabeled. Holthuis (1959) restricted the type locality to Guadeloupe because material examined by Herbst, following Slabber's description, was collected from Guadeloupe.

The binomial nomenclature introduced by Linnaeus (1758) was used by Herbst (1788:229) to designate the species *Cancer seticornis*. His abbreviated description was based on the work and material of Slabber and even reproduced the figure used by Slabber (Herbst, 1788: tabl. XVI, fig. 91). As noted by Yang (1967:211), this figure was also reproduced by Bosc (1802). A more detailed and accurate representation of a male *Stenorhynchus* species was later given by Herbst (1803: tabl. LV, fig. 2) from Guadeloupe material. This latter figure shows the rostrum nearly twice the length of the postorbital carapace. The margins of the rostrum are nearly parallel, and the relative length of the dactyl of the cheliped suggests that the specimen figured represents *S. seticornis*. However, the very regular placement of spines and absence of postocular spines indicate that the figure is somewhat stylized and not an accurate representation.

The type material for *S. seticornis* has not been located and must be assumed lost or destroyed. Slabber's original material was offered for sale to the "Zeeuwsch Genootschap van Wetenschappen" (Society of Sciences of the Province of Zeeland) in Middelburg, the Netherlands. The price asked was not agreeable and the offer was declined. The collection later reputedly was sold to the Leiden Museum. No record of this acquisition exists and no material is present which can be attributed to Slabber's "Sea Crab." The type specimens must be assumed lost (L. B. Holthuis, pers. comm.).

Because the original type locality is in error and the original description lacks diagnostic features, a neotype is proposed for the redescription of *S. seticornis*. The specimen on which the redescription is based was collected from the Dutch West Indies, Curaçao (USNM 42956). The previously designated type locality of Guadeloupe (Holthuis 1959)

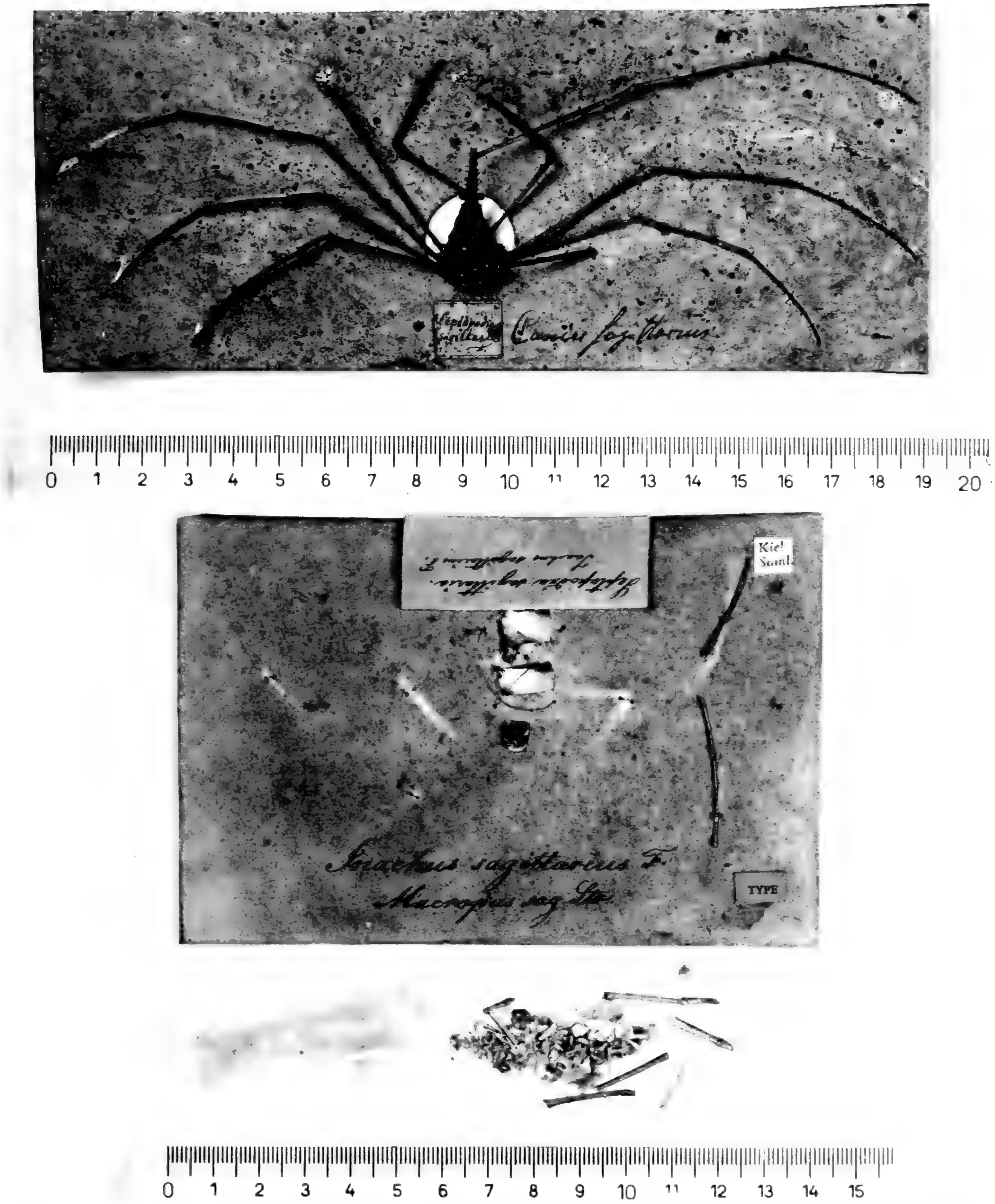

Fig. 2. *Cancer sagittarius* Fabricius, 1793: Above, "Type" specimen from the Copenhagen Museum; Below, the specimen originally deposited in the Kiel Museum.

is superseded by Curaçao with the selection of the male neotype. Curaçao is a location from which collectors are known to have sent Slabber material for examination (Holthuis, pers. comm.).

The second name to be considered is *Cancer sagittarius* (Fabricius, 1793). The original description of *Cancer sagittarius* is inconclusive. However, from an examination of the syntypes, it has been confirmed the Fabrician material is conspecific with *Stenoyrhynchus seticornis*. A syntype was originally deposited in the Zoological Museum, Copenhagen, and a second syntype, along with the remainder of the Fabrician material, has been transferred from the Kiel Museum to Copenhagen. The syntype of *Cancer sagittarius* transferred from the Kiel Museum has deteriorated to fragments that are very nearly unrecognizable. This specimen (Fig. 2) was listed by Rathbun (1925: 14) as type material. However, it was not listed by Zimsen (1964) as a syntype. Prof. Torben Wolff (Zoological Museum, Copenhagen) knows no reason why one specimen was listed as the type by Zimsen and not both (pers. comm.). This female syntype possesses all the characters listed below as typical of *S. seticornis*.

The eastern Atlantic species of *Stenorhynchus* was considered conspecific with the western Atlantic species until Yang (1967, 1976) showed it to be distinct. Apart from the unavailable *Leptopodia vittata* Kingsley, two names have been applied to the eastern Atlantic form, *Leptopodia lanceolata* Brullé, 1837, and *L. canariensis* Brullé, 1839, both described from the Canary Islands. As Yang pointed out, the correct name for the eastern Atlantic taxon is *Stenorhynchus lanceolatus* and *L. canariensis* must be considered a junior synonym. Yang (1967) showed how *S. lanceolatus* differs from both *S. seticornis* and the proposed new species and Manning & Holthuis (1981) presented considerable data on the biology and distribution of *S. lanceolatus*. Paula (1987) has most recently described the first zoeal stage of *S. lanceolatus* and compared it with the works of Yang (1967, 1976).

The next name possibly available is *Leptopodia ornata* Guilding, 1825, described from St. Thomas in the Caribbean Sea. The original description in Latin is very brief. It treats a majid crab with a serrate rostrum, and includes few details as to general shape of the legs or other features. Guilding also corrected the definition of *Leptopodia* by detailing the arrangement of the abdominal segments. By today's standards, however, there are no characters described for *L. ornata* that are of diagnostic value. Rathbun (1925) listed the type specimen of *L. ornata* as not in the British Museum and perhaps not extant. Yang (1967) requested Dr. Isabella Gordon to make another search for the specimen, but that search was also fruitless and the type must be assumed lost. *Leptopodia ornata* Guilding, 1825, is herein designated a junior synonym of *Stenorhynchus seticornis* (Herbst, 1788).

Another name in the literature which may have precedence for the proposed new species is *Leptopodia vittata*. Kingsley (1880) reported the presence of a specimen within the collections of the Museum of the Academy of Natural Sciences of Philadelphia labeled "*Leptopodia vittata* Guer., Senegal." He stated that it might represent a manuscript name and that no published description could be found of the species. *Leptopodia vittata* Kingsley, 1880, is not available because it was published only in synonymy and was not adopted before 1961 as a name for a species. Manning & Holthuis (1981) listed this species as synonymous with the West African *S. lanceolatus* Brullé, 1837.

Goeldi (1886) described *Leptopodia lineata* from Rio de Janeiro and Cabo Frio, Brazil. The description is somewhat vague, not detailed enough to determine which of the 2 western Atlantic species it represented, and the illustrations are not sufficiently detailed to accurately identify the taxon by today's standards. An attempt to locate the type series of *L. lineata* at the major zoological museums of Europe and Brazil was fruitless; the type must be assumed lost. *Stenorhynchus* material obtained from Cabo Frio and Rio de Janeiro revealed only *S. seticornis*. A search by Dr. W. Zwink (Museu Nacional, Rio de Janeiro) of holdings of local specimens of *Stenorhynchus* showed no representatives of a second species. It may be conclusively presumed that this taxon is conspecific with *S. seticornis* and is herein designated a junior synonym.

The only remaining specific name that needs to be mentioned here is *Pactolus bosci*, Leach, 1815. This species was based on a single specimen of unknown origin found in the holdings of the British Museum (Natural History). As the name has been suppressed by the ICZN (opinion 763) it is not available for use.

Systematics

Due to the extremely common nature of *Stenorhynchus* species and their wide geographic range, it is nearly impossible to detail all of the workers who have dealt with western Atlantic members of the genus in the past 200 years. It is not attempted here. In most cases, it is not feasible to determine accurately from the literature which of the two species was the subject of each report. A great many of the citations are species listings and not accompanied by diagnoses, ecological data, or illustrations which would help to determine the identity of the taxon reported. However, a few records are sufficiently detailed (e.g., Hay & Shore 1918; Williams 1965, 1984) or have illustrations which help to clear up some of the confusion. For these reasons, the synonymies that follow are abbreviated and by no means detailed accounts of references to *Stenorhynchus* species in the literature.

The materials examined in the following species accounts are housed at the United States National Museum of Natural History (USNM), Florida Department of Natural Resources, Marine Research Laboratory (FSBC), Museu Nacional, Rio de Janeiro, Gulf Coast Research Laboratory (GCRL), Dauphin Island Sea Lab (MESC), and the University of Southwestern Louisiana (USLZ).

Stenorhynchus seticornis (Herbst, 1788), redescription

Figs. 1a, b, d–g, 2, and 3

Oost-Indische Zee-Krabbe Slabber, 1778: 162, pl. 18, fig. 2.

Cancer seticornis Herbst, 1788:229, pl. 16, fig. 1; & 1803:27, pl. 55, fig. 2.

Cancer sagittarius Fabricius, 1793:442.

Leptopodia ornata Guilding, 1825:335.

Leptopodia lineata Goeldi, 1886:37, pl. 3, figs. 24–31.

Stenorynchus sagittarius.—Rathbun, 1901: 53.—Hay & Shore, 1918: 455, pl. 37, fig. 8 (in part).

Stenorynchus seticornis.—Rathbun, 1925: 14, pls. 2 and 3 (in part).—Abele, 1970: 137 p.

Stenorhynchus seticornis.—Williams, 1965: 244, figs. 222 and 223K (in part).—Felder, 1973:48, pl. 7, fig. 1.—Yang, 1976.—Felder & Chaney, 1979:27.—Wicksten, 1980:150.—Williams, 1984:304 (in part).

Material examined.—Table 1.

Diagnosis.—Carapace naked, rostrum covered with short dense felt and setae, becoming longer and thicker distally. No spines at distal end of basal antennal article, single inter-antennular spine directed posteriorly. Chelipeds hairy, palm from three to four times length of fingers in mature males, not as stout in females. Merus of third maxilliped normally with small spine on anterodistal angle. Pereopods, abdomen, and sternum bearing short pubescence.

Description of male neotype (USNM 42956).—Carapace subtriangular, smooth, naked, regions slightly defined; intestinal and cardiac region inflated and separated by shallow furrow from posterior regions; branchial region inflated, delimited by shal-

Table 1.—Material examined; *Stenorhynchus seticornis.*

Catalog number	Location	Material	Depth (m)
USNM 42956 (Neotype of *Stenorhynchus seticornis*)	Curaçao, Suriname	1 ♂	—
USNM 19941	Rio de Janeiro, Brazil	1 ♂	—
USNM 76441	Gallows Bay, St. Croix, Virgin Islands	1 ♂	—
USNM 46697	Aucilla, FL	1 ♀	13
USNM 43065	Montego Bay, Jamaica	2 ♂	—
USNM 43066	Jamaica	1 ♂	—
USNM 19580	Kingston Harbor, Jamaica	1 ♂	—
USNM 31040	Grolding Cay, Bahamas	1 ♂	—
USNM 11232	33°34′N, 77°42′W	1 ♂, 1 ♀	16.5
USNM 19940	Bay of Bahía, Brazil	1 ♀	—
USNM 22554	Santa Marta, Colombia	1 ♂	—
USNM 69601	18°30′N, 66°04′W Puerto Rico	1 ♂	366
USNM 101712	16°05′N, 82°05′W	1 ♂	44
USNM 137761	Grand Island, Trinidad	3 ♂	69
USNM 137020	00°15′S, 46°45′W	1 ♂, 2 ♀	28
USNM 171562	Tongue of the Ocean, Bahamas	1 ♂	—
USNM 184122	Palm Beach, FL	1 ♂	22
USNM 58047	Shoal Banks, Barbados	1 ♂	55
USNM 154711	Grenada	1 ♂	—
USNM 321390	Belize	1 ♀	—
USNM 103268	06°51′N, 54°53′W Suriname	1 ♀	51
USNM 43060	Montego Bay, Jamaica	1 ♂	—
USNM 105004	08°40′N, 77°10′W Gulf of Darien	1 ♀	61
USNM 137020	00°15′S, 46°45′W Para, Brazil	1 ♂, 1 ♀	27
USNM 107804	off Houma, LA	1 ♂	—
USNM 103267	06°49′N, 55°54′W	1 ♀	47
USNM 103504	07°40′N, 57°34′W	1 ♂	—
USNM 17374	22°18′N, 87°04′W	1 ♂	44
USNM 49082	10 miles south of Key West, FL	1 ♀	229
USNM 42955	Curaçao	1 ♀	—
USNM 101713	01°50′N, 47°31′W	1 ♀	85
USNM 43062	Montego Bay	1 ♂	—
USNM 7653	St. Thomas	1 ♂	—
USNM 17373 (in part)	35°08′30″N, 75°10′W	1 ♂	90
USNM 137019	04°46′N, 51°21′W	1 ♂	59
USNM 103265	06°48′N, 54°54′W	2 ♂	46
MESC 6187-0121	28°26′N, 84°21′W	3 ♂, 3 ♀	—
MESC 6187-0113	28°25′N, 84°19′W	6 ♂, 4 ♀	—
MESC 6187-0114	30°02′30″N, 86°06′30″W	2 ♂	31
MESC 6187-0109	28°36′N, 84°16′W	7 ♂, 5 ♀	—
GCRL I64:695	29°43′N, 88°26′W	1 ♂, 3 ♀	—
FSBC I 31042 (in part)	30°30′N, 80°15′W	2 ♀	47
FSBC I 31045 (in part)	30°20′N, 80°14′W	1 ♂	65
FSBC I 31043 (in part)	30°31′N, 80°10′W	1 ♂, 2 ♀	64
FSBC I 31044 (in part)	30°20′N, 80°17′W	1 ♀	46
FSBC I 31032	27°40′N, 80°06′W	1 ♀	27
FSBC I 31030	27°10′N, 80°01′W	1 ♀	46
FSBC I 31029	27°10′N, 80°01′W	1 ♀	45
Museu Nacional Rio de Janeiro	Cabo Frio, Brazil	1 ♂, 1 ♀	—
Museu Nacional Rio de Janeiro	Rio de Janeiro, Brazil	1 ♂, 1 ♀	—
Museu Nacional Rio de Janeiro	Guanabara, Brazil	1 ♂, 1 ♀	—

low margin; hepatic region inflated, with well-defined ventral margin, but remaining ventral margin ill defined. Simple, strong deflexed postorbital spine; supra-orbital furrow shallow; rostrum flattened basally between eyes; short setae from base of rostrum to tip, setae dense and increasingly long distally; subhepatic region inflated posteriorly, margins well defined; 1st rostral spine directed laterally, slightly deflexed, followed by up to 16 large spines on lateral margins, directed forward and occasionally downward; rostrum 1.8 times length of carapace behind transverse line connecting base of eyestalks dorsally. Basal antennal article elongate, with longitudinal ventral furrow, strong spine anterolaterally directed on ventral margin; septum dividing antennular sinuses with posteriorly directed spine; anterolateral margin of sinus defined by upturned border; lateral and anterior margins of buccal cavity with raised ridge, acute small spine at anterolateral angle of mouth frame. Exopod of third maxilliped with maximum width one-third distance from base, narrowing distally; internal margin of merus straight, with strong spine at anteromesial angle and small spine on exterior margin posterior to articulation with palp.

First pereopods greatly elongate, covered with short dense pile; basis inflated, tuberculate, with spine on interior margin; merus tuberculate, with region of few tubercles dorsolaterally, six to nine strong spines on mesial row, single spine dorsally, two spines in lateral row, ventral spine toward distal margin, three or four spines at articulation with carpus; carpus with three strong spines dorsally, three distal spines ventrally and numerous tubercles; propodus covered with strong tubercles and low pile which becomes denser and longer at base of finger, pile extends laterally along propodus and onto ventral surface at base of finger, propodus three times length of dactyl; dactyl stout, with long dense setae dorsally and laterally at base, thinning distally to become sparse long setae, tuberculate dorsally.

Second pereopod longer than first and covered with short dense pile; merus with 4 longitudinal rows of spines, 5 or 6 spines in dorsal row, 5–7 spines in lateral row concentrated in distal ½, 11 mesial spines distributed along length of segment, 2 ventral spines in distal ½; 3 spines at articulation with carpus slightly longer than others; carpus with pair of dorsal spines at midlength and 3 spines at articulation with propodus longer than others; length of carpus and propodus equal to dactyl but shorter than merus; propodus with 11–13 spines, slightly compressed laterally, 2 spines at articulation ventrolaterally; dactyl elongate, slightly curved, little compressed laterally, with 5 longitudinal rows of setae.

Third pereopod shorter than second, covered with short dense pile; merus with 5 dorsal spines along length, 8–10 spines along inner row, 3–4 spines in distal ½ on external row, single spine on ventral margin in distal ½, 3 spines at articulation with carpus; carpus with pair of dorsolateral spines at midlength and 3 spines at articulation with propodus; propodus with 11–13 small spines, slightly compressed laterally, with 2 spines at articulation; dactyl ⅘ length carpus and propodus combined, with 5 longitudinal rows of setae, curved slightly in distal ½.

Fourth pereopod shorter than third, with covering of short pile; merus with four to five spines on internal row and ventrolateral spine at articulation slightly enlarged; carpus with pair of dorsal spines at midlength and three spines at articulation with propodus; propodus with eight or nine small spines; dactyli damaged, slightly compressed laterally, and bearing five longitudinal rows of setae.

Fifth pereopod shorter than fourth, covered with short dense pile; merus with 4 dorsal spines, single ventrolateral spine and 2–4 mesial spines; carpus with pair of spines dorsolaterally at midlength, 3 terminal spines at articulation; propodus with 9–10 low spines, slightly compressed; dactyl elongate, curved distally with 5 rows of longitudinal setae.

Abdominal segments 5 and 6 fused, with sutures indicated; segment 1 slightly longer than wide, naked along elevated midlength but with setae in depressions; segments 3 and 4 subequal, longer than 2; 3 widest anteriorly, segments 5 and 6 fused, segment 7 is 1.75 times long as wide with hollowed protuberance for locking mechanism and a small tubercle medially in proximal one-half. Sternum with 22 large tubercles and few low setae; sternite 5 with 2 tubercles at articulation with basis of maxilliped; sternite 4 with 8–9 tubercles at articulation with first pereopod; plastron with arcuate ridge in anterior ½ lined with setae, lateral margin parallel.

Color.—Carapace with alternating stripes of off-white and brown-maroon, white stripes on dorsum of carapace reminiscent of inverted V's, large white bands originating dorsally between fourth and fifth legs join anterior to eyes, every other white stripe smaller than preceding; white bands originating at tip of dactyl of pereopods, continuing dorsally along leg onto carapace, or originating at posterior margin of carapace between coxae of legs. Carapace with 4 major white longitudinal bands, one running along the pterygostomial ridge. Distal ⅔ of fingers on chelae blue. Inner surface of fingers each with 2 whitish spots, forming rough circle when fingers close. Merus of cheliped with large orange-yellow spot at base of distal spine. White band bordered with maroon extending obliquely across merus and palp of third maxilliped. Broad yellow-white band connecting coxae of first pereopods with area under third maxilliped.

Range.—Material assignable to *S. seticornis* has been examined from Cape Fear, North Carolina, through the Gulf of Mexico southward to the mouth of the Amazon River, and Cabo Frio, Brazil. Bathymetric records are from 1 to 366 m.

Remarks.—The above technical description is drawn from the designated neotype, a mature male collected at Curaçao, Dutch West Indies. This specimen is the form commonly found on the rock outcroppings or coral reefs in temperate and tropical waters of the western Atlantic, and reported by Herbst (1803) from Guadeloupe.

Variation.—*Stenorhynchus seticornis* exhibits considerable morphological variation which appears to be related to the substrata from which the specimens are collected. One variant, herein designated *S. seticornis* form A, is most often collected on hard rocky bottoms (i.e., rock outcroppings, reefs, jetties) or immediately adjacent to these hard-bottom types. It is a large heavy bodied form, having an extremely long rostrum with subparallel margins throughout most of the length. This form was mentioned by Yang (1967) as "atypical."

Stenorhynchus seticornis form B differs from the above by characters enumerated below. Form B is the ecotype most often found in the northern Gulf of Mexico on mud bottoms and in grass beds. It was listed by Yang (1967, 1976) as *Stenorhynchus seticornis* and the complete larval development has been described. It is the smaller of the two forms. In SEM micrographs, the male pleopod of *S. seticornis* form A (Fig. 3) shows little variation, other than size, from that of *S. seticornis* form B (Fig. 3). The somewhat narrower opening of the apex and the slightly shorter apex may represent differences in the orientation of the gonopod at the point where the photographs were taken. This very minor difference, and the observed gradation between the two forms, are well explained by ecophenotypic variation.

Stenorhynchus seticornis form B is separated from *S. seticornis* form A by: 1) smaller overall body size, 2) females and subadult males with large hiatus at base of moveable fingers, and 3) setae on the dactyl and propodus of the first leg not forming thick mat continuous on dorsal surface.

Considerable intergradation is found between the two forms of *S. seticornis*, espe-

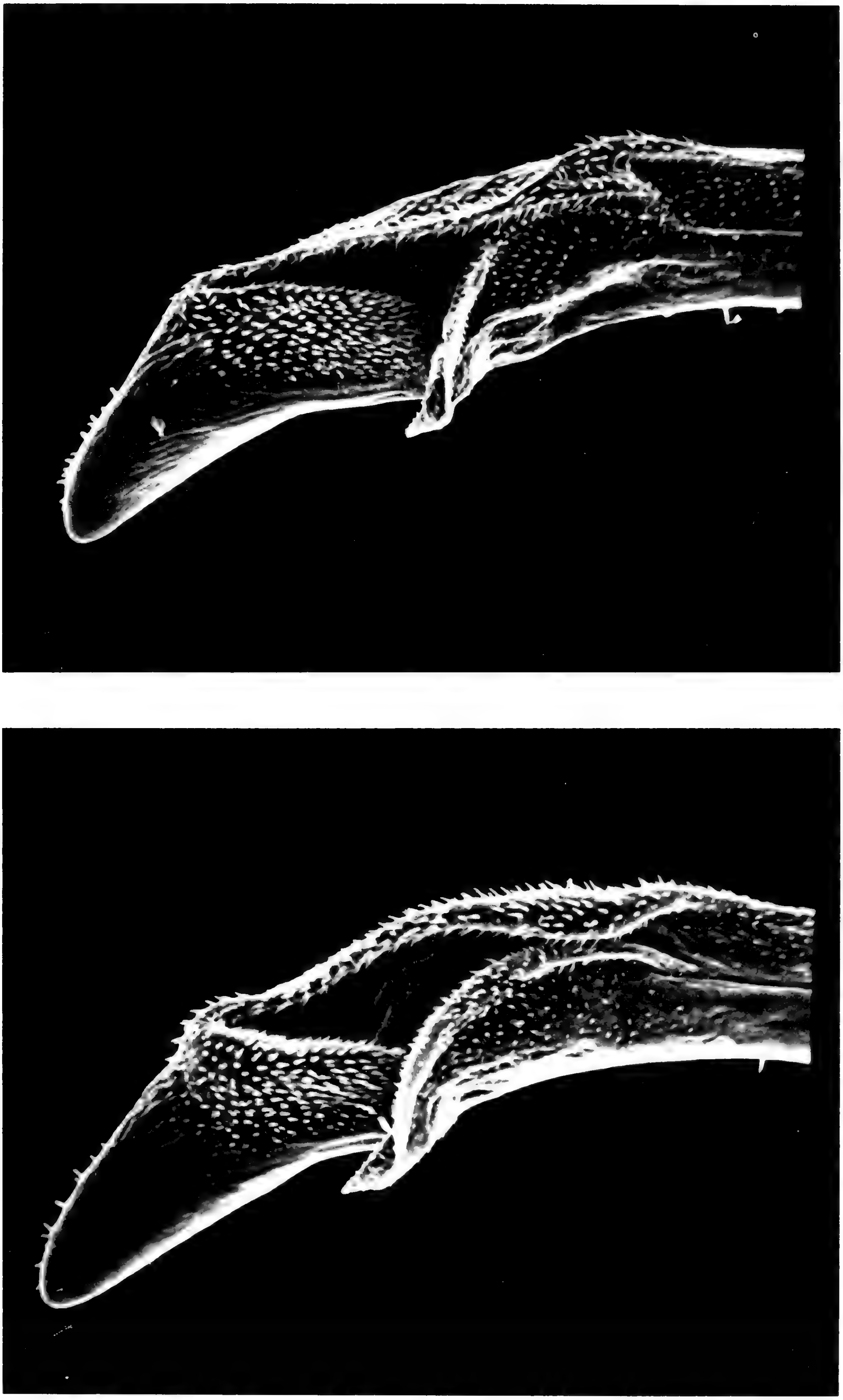

Fig. 3. Scanning electron micrographs of the tips of male gonopods: Above, *Stenorhynchus seticornis* form A; Below, *S. seticornis* form B.

Table 2.—Material examined; *Stenorhynchus yangi.*

Catalog number	Location	Material	Depth (m)
USNM 211812 (HOLOTYPE)	33°49'N, 76°43'W	1 ♂	81
USNM 211855 (PARATYPE)	26°45'70"N, 84°00'13"W	1 ♂	89
USNM 211803 (PARATYPES)	33°48'46"N, 76°35'W	3 ♂, 2 ♀	60
USNM 67800	18°30'30"N, 66°23'50"W	1 ♂	73
USNM 101715	34°17'N, 76°01'W	1 ♀	137
USNM 120135	Dominican Republic	1 ♀	—
USNM 103269	6°52'N, 54°53'W	1 ♂, 1 ♀	288
USNM 73401	Barbados	1 ♂	—
USNM 73086	Grand Cayman	1 ♂	220
USNM Uncatalogued Oregon St. 4391	12°33'N, 71°09'W	1 ♂, 1 ♀	73
USNM Uncatalogued Oregon St. 3605	12°16'N, 82°53'W	1 ♂	73
USNM 69601	18°30'30"N, 66°04'05"W	1 ♂	365
USNM 92646	21°15'N, 92°16'W	1 ♂	64
USNM 211815	33°48'42"N, 76°34'12"W	1 ♂, 1 ♀	102
USNM 24418	Mayaguez Harbor, Puerto Rico	1 ♂	137
USNM 11379	Key West, FL	1 ♀	108
USNM 11219	Martha's Vineyard	1 ♂	62
USNM 211807	33°47'36"N, 76°34'24"W	2 ♀	116
USNM 9496	Key West	1 ♂, 1 ♀	—
USNM 103504	70°40'N, 57°34'W	1 ♀	—
USNM 6934	9°30'15"N, 76°20'30"W	3 ♂, 3 ♀	—
USNM 9862	33°18'30"N, 77°07'W	1 ♂	174
USNM Uncatalogued Oregon St. 4391	12°33'N, 71°09'W	1 ♂, 1 ♀	73
USNM Uncatalogued Oregon St. 3605	12°16'N, 82°53'W	1 ♂	73
USNM 17373 (in part)	35°08'30"N, 75°10'W	2 ♀	90
GCRL I60:165	25°35'N, 83°42'W	5 ♂, 7 ♀	110
FSBC I 31031	27°40'N, 79°59'W	2 ♂, 1 ♀	64
FSBC I 31049	30°00'N, 80°15'W	1 ♂	91
FSBC I 31042 (in part)	30°30'N, 80°15'W	1 ♀	47
FSBC I 31048	30°11'N, 80°15'W	1 ♂	64
FSBC I 31033	27°50'N, 79°58'W	1 ♂, 1 ♀	92
FSBC I 31045 (in part)	30°20'N, 80°14'W	10 ♂, 4 ♀	65
FSBC I 31041	30°40'N, 80°06'W	2 ♂, 1 ♀	91
FSBC I 31036	28°40'N, 80°06'W	1 ♀	64
FSBC I 31043 (in part)	30°21'N, 80°10'W	1 ♂, 1 ♀	64
FSBC I 31046	30°20'N, 80°12'W	1 ♂	92
FSBC I 31040	30°40'N, 80°07'W	1 ♂	64
FSBC I 31037	28°50'N, 80°09'W	1 ♂	64
FSBC I 31034	28°30'N, 80°01'W	1 ♀	91
FSBC I 31047	30°10'N, 80°14'W	1 ♀	91
FSBC I 31038	29°00'N, 80°10'W	1 ♀	64
FSBC I 31044 (in part)	30°20'N, 80°17'W	1 ♀	46

cially in areas of rock outcroppings adjacent to muddy bottoms. In this situation, specimens are larger than those found on muddy bottoms, but often possess the hiatus at the base of the fingers and the greatly elongated rostrum of the form common to reefs. Similarly, specimens from grass beds adjacent to coral heads exhibit characteristics of both forms A and B.

Specimens of *S. seticornis* exhibit great variation in a number of characters, including length of the rostrum and the fingers. To document this variation, I measured the total postorbital carapace lengths and total carapace lengths on specimens for which the rostrum was unbroken on specimens which represented the entire geographic range. The postorbital measurement was determined from the posterior margin of the carapace to a point midway between the base of the eyestalks. Additional measurements of the moveable finger and palm length were taken. The range of the ratio of postorbital length to total carapace length is slightly different in males (n = 20:0.27–0.40) and females (n = 5:0.33–0.42), but no real dimorphism in carapace dimensions is evident which is attributable to the sex of the specimens. These differences bear no relationship to either the size of the individual or the location from which it was collected. However, differences in the range of ratios of the finger to palm lengths do seem attributable to sexual dimorphism. Although there is some overlap in the range, males (n = 22) tend to have shorter fingers, relative to the palm length (0.24–0.39) than do females (n = 7:0.37–0.45). This trend is also evident in *S. yangi*.

A detailed examination of the variation found in *S. seticornis* has not produced sufficient data to warrant the establishment of separate subspecies. Until the larval development of *S. seticornis* form A has been documented, I prefer the designation "form" to a questionable subspecies status.

Stenorhynchus yangi, new species
Fig. 1c

Stenorynchus sagittarius.—Hay & Shore, 1918:455, pl. 37, fig. 8 (in part).

Stenorynchus seticornis.—Rathbun, 1925: 14, pls. 2 and 3 (in part).

Stenorhynchus seticornis.—Williams, 1965: 244, figs. 222 and 223K (in part).—1984: 304 (in part).

Stenorhynchus sp. A.—Yang, 1967; 459 p.—1976:158.

Material examined.—Table 2.

Diagnosis.—Carapace naked, rostrum devoid of setae or felt; no spines at distal end of basal antennal article; interantennular septum without posteriorly directed spinous process; chelipeds hairy, palm only twice length of moveable fingers in males, 1.5 to 2 times length of dactyl in females. Merus of third maxilliped with vestigial spine at anteromedial angle. Ambulatory legs, abdomen and sternum without pubescence. Regions of carapace well defined and inflated.

Description of holotypic male (USNM 211812).—Carapace subtriangular, smooth, naked, regions well defined; branchial regions inflated; intestinal and cardiac regions elevated in midline and separated from branchial and cardiac regions by sulcus; gastric region inflated; hepatic region moderately inflated and defined by furrows on all sides. Strong postorbital tooth bifid, deflexed and directed slightly forward. Shallow supraorbital furrow; rostrum flattened between eyestalks, devoid of setae; subhepatic region inflated posteriorly with well defined margins; first rostral spine directed slightly forward; rostrum about equal to length of postorbital carapace, naked, broad basally and tapering to acute apex, bearing 17 to 19 large lateral spines; basal antennal article with shallow longitudinal furrow and strong anteriorly directed spine on ventral margin; septum dividing antennular sinuses well developed, with rounded ventrum; anterolateral margin of sinus simple. Lateral and anterior margins of buccal frame with raised margin and weak spine at anterolateral angle; exopod of third maxilliped with maximum width at one-half length from base, narrowing distally, internal margin of merus concave, occasionally with small spine at antero-internal angle, small spine posterior to articulation with palp.

All pereopods with few scattered setae. First pereopod greatly elongate; ischium slightly inflated, smooth; merus with numerous spines in longitudinal rows; two spines in distal one-half of lateral row; three spines in dorsal row evenly spaced, enlarged terminal spine at articulation with carpus; six spines on interior row; carpus with two dorsal spines at midlength and pair of terminal spines ventrally; propodus with small scattered tubercles. Felt and dense setae laterally at base of finger in small patch with longer sparse setae on immoveable finger;

dactyl with small patch of setae at base, with few long scattered setae on surface, small hiatus at base.

Second pereopod elongate, longer than first; ischium very short, tuberculate dorsally; merus greatly elongate, with about 20 spines arranged in 4 longitudinal rows, 3 larger terminal spines; carpus short, about ⅕ length of merus, with 3 dorsal and 3 terminal spines; propodus elongate, ¾ length of merus, with numerous spinules and tubercles, 1 lateral terminal spine; dactyl elongate, ⅘ length of merus, slightly compressed laterally, lined with spinules and with corneous tip.

Third pereopod shorter than second; ischium very short, tuberculate; merus elongate, with approximately 15 spines arranged primarily in 2 dorsal rows, 3 terminal spines; carpus short, ¼ length of merus, 3 dorsal and 3 terminal spines; propodus elongate, ⅔ length of merus, with approximately 10 dorsal and 2 terminal spines; dactyl elongate, ⅘ length of merus, with numerous spinules, slightly compressed laterally with corneous tip.

Fourth pereopod shorter than third, ischium tuberculate, very short; merus elongate, roughly 20 spines arranged in 2 primary dorsal rows, 3 terminal spines; carpus short, ¼ length of merus with 3 dorsal and 3 terminal spines; propodus elongate, ⅔ length of merus with about 10 spines dorsally and 3 terminal spines; dactyl elongate, ⅘ length of merus with numerous spinules and corneous tip, slightly compressed laterally.

Fifth pereopod shorter than fourth, ischium very short, slightly tuberculate; merus elongate, with 10 spines in 2 dorsal rows, and 3 terminal spines; carpus short, ⅓ length of merus, with 3 dorsal and 3 terminal spines; propodus elongate, equal in length to merus, with spinules mainly in single dorsal row, slightly compressed laterally, numerous spinules along length; dactyl with corneous tip.

First abdominal segment little longer than wide, elevated along midline, segments 2 and 3 very short but broad; segments 4 and 5 somewhat longer and constricting to narrowest part of abdomen, segments 6 and 7 fused, no external indication of fusion visible. Tubercles scattered on sternum with very few setae apparent; anterior extension of sternum with ridge below mouth frame bearing setal row and two spines at center of process.

Color.—Carapace with four triangular white stripes, yellow and orange-reddish-brown areas surrounding white stripes. Lateral white stripe passes through orbital area and is continued onto lateral edge of rostrum. Lateral teeth of rostrum white; tip of rostrum dark brown. Fingers of cheliped purple for distal two-thirds to three-fourths of length, teeth white, remainder of fingers tan; carpus tan with brown stripe proximally; merus dark brown distally, pale yellow spot behind large distal tooth. Ambulatory legs with faint light dorsal stripe continuous from carapace, distal ends of segments darker, merus with darker areas; dactyli with distal ⅓ white, apex translucent with penultimate tan band and then white. Legs with faint dark/light bands.

Range.—*Stenorhynchus yangi* has been collected from Martha's Vineyard south through the Gulf of Mexico to Suriname in depths from 31 to 365 m.

Variation.—Within *S. yangi*, variation has been noted in the shape of postorbital spines, characteristic robustness of the carapace and relative lengths of the rostrum and moveable finger of the first leg. Williams (1965:244) reported the postorbital spine of *S. seticornis* as "occasionally bifid." During the course of this study, no specimens of *Stenorhynchus seticornis* were observed which possessed bifid postorbital spines. However, it is common to come across large specimens of *S. yangi* with this condition. Several large individuals of *S. yangi* were examined which had single and double spines on alternate sides of the carapace. Specimens with trifid spines were also observed, and it is probable that the individuals reported by Williams (1984) with bifid spines represent *S. yangi*, as the gonopod figured in that work (fig. 2410) corresponds with *S. yangi*, not *S. seticornis*. The characteristic robustness or swelling of the various regions of the carapace also varies within *S. yangi*. This and the relative lengths of the pereopods are probably related to maturity of the individual. Considerable variation was also noted in spination of the pereopods.

Perhaps the two features which exhibit the greatest degree of variation are the ratio of total carapace length to postorbital carapace length and the ratio of finger to palm length of the first pereopod. Only individuals with the rostrum intact (n = 29) were used for carapace length measurements, with individuals from the extreme ends of the geographic range included. Among males (n = 19), the postorbital carapace length accounted for one-fourth to one-half of the total length of the individual (0.27–0.49); little difference from this ratio was noted among females (0.31–0.48). However, the range ratio of finger to palm length was notably different among males (n = 22:0.24–0.39) and females (n = 13:0.36–0.49).

A single anomaly was noted in a specimen from the Caribbean (USNM Accession #42869). This individual is a mature male with a bifid rostrum, but is normal in all other respects.

Etymology.—It is my pleasure to name this species for Dr. Won Tack Yang (Texas Biomedical Institute) who, on the basis of larval characters, first recognized the possibility of its distinctness.

Remarks.—Yang (1967, 1976) performed much of the complicated work involved in reviewing the confused history of this genus and gave definitive proof that at least two species of *Stenorhynchus* are present in western Atlantic waters. His work was the first to correct the mistaken records of *S. seticornis* in the eastern Atlantic and showed *S. lanceolatus* Brullé, 1837, to be the correct name for the West African species.

Yang (1967) indicated that *S. yangi* may be a deep water species and presented data which appeared to show that the species was most often collected in waters deeper than 65 m. He noted that in the collections at the University of Miami Marine Laboratory and those examined from the U.S. National Museum of Natural History, this species' bathymetric range was from 31–119 m. He suggested the possibility of an isotherm dividing the preferred habitats of the two species. Abele (1970) indicated a restricted occurrence of *S. yangi* to waters over 50 m. However, because I have not re-examined that material, that report of the species encountered is unconfirmed.

The robust nature of the carapace of this species, the absence of the interantennular spine, the lack of rostral setation, the shape of the first male pleopod and the form of the spermathecae of the female easily distinguish *S. yangi* from *S. seticornis*. Differences in the color patterns of the two species also aid in their identification; however, this difference may be quickly obscured by preservation techniques and be of little use to the researcher studying museum specimens. Differences in relative lengths of the ambulatory legs may also be of aid in the separation of *S. yangi* from *S. seticornis*. However, the fragile nature of members of this genus makes studies of this type very difficult as legs are rarely collected intact.

Discussion.—Taxonomic confusion surrounding the identity of *S. seticornis* and *S. yangi* is partly due to the great amount of variation found within the two taxa. The range of variation in the ratio of postorbital to total carapace lengths differs little from *S. seticornis* (0.27–0.49) to *S. yangi* (0.27–0.42). A broad range of variation is also evident in the ratio of finger to palm length (0.24–0.49 in *S. seticornis* and 0.24–0.45 in *S. yangi*).

Because of the taxonomic problems, ecological works that have dealt with this group must be used with reserve. Bathymetric records (Rathbun 1925), distributional records (Holthuis 1959; Williams 1965), substrate preferences (Rathbun 1925) and ecological and behavioral works (Hartnoll 1965; Barr 1971, 1975) must all be viewed with caution and records re-examined where feasible. Although the specific identity of the arrow crabs used in the reproductive studies may be of little significance in the understanding of the group's behavior, it must be recognized that doubt exists as to which taxon was being studied by Schone (1968). Barr's (1971, 1975) field work suggests that *S. seticornis* is a facultative filter feeder which climbs to the top of an outcropping or reef at dusk. By sitting motionless, the crab allows the passing debris to collect on the setae of its body during the night, and the following day is spent cleaning off the entrapped food. No data were given by that author to indicate the frequency of this feeding mode. R. H. Gore (pers. comm.) noted that in aquaria, *S. seticornis* will snip off and eat the protruding siphon of the gastropod *Nassarius vibex*. Mary K. Wicksten (pers. comm.) has indicated that *S. seticornis* may perform an unusual decorating act by storing food gathered from the substratum on the rostral setae to be eaten later. This is a modification of the usual decoration behavior used for concealment and camouflage (Wicksten 1980). An alternative feeding behavior is dictated for *S. yangi* because of the lack of rostral setae. No study has been accomplished to define the niche requirements of these two species and how these requirements may differ.

The complete larval development of *S. seticornis* form A was described by Yang (1967, 1976). He detailed three zoeal stages and the megalopa obtained from females collected in Biscayne Bay, Florida. Yang (1967) specifically mentioned the hiatus at the base of the fingers, a character previously listed as useful in separating the two forms of *S. seticornis*. A single zoeal stage of *S. yangi* (*Stenorhynchus seticornis* of Yang 1967, 1976) was described from a specimen collected in about 225 m of water. The larvae of the two species are sufficiently distinct to allow quick separation of the species because of a large lateral bifurcation on the carapace of *S. yangi*. This situation is unusual in that the adults are similar enough to have been united under a single name for many years, but the larvae are quite different at the first zoeal stage.

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HOBBSEUS YALOBUSHENSIS, A NEW CRAWFISH FROM CENTRAL MISSISSIPPI (DECAPODA: CAMBARIDAE)

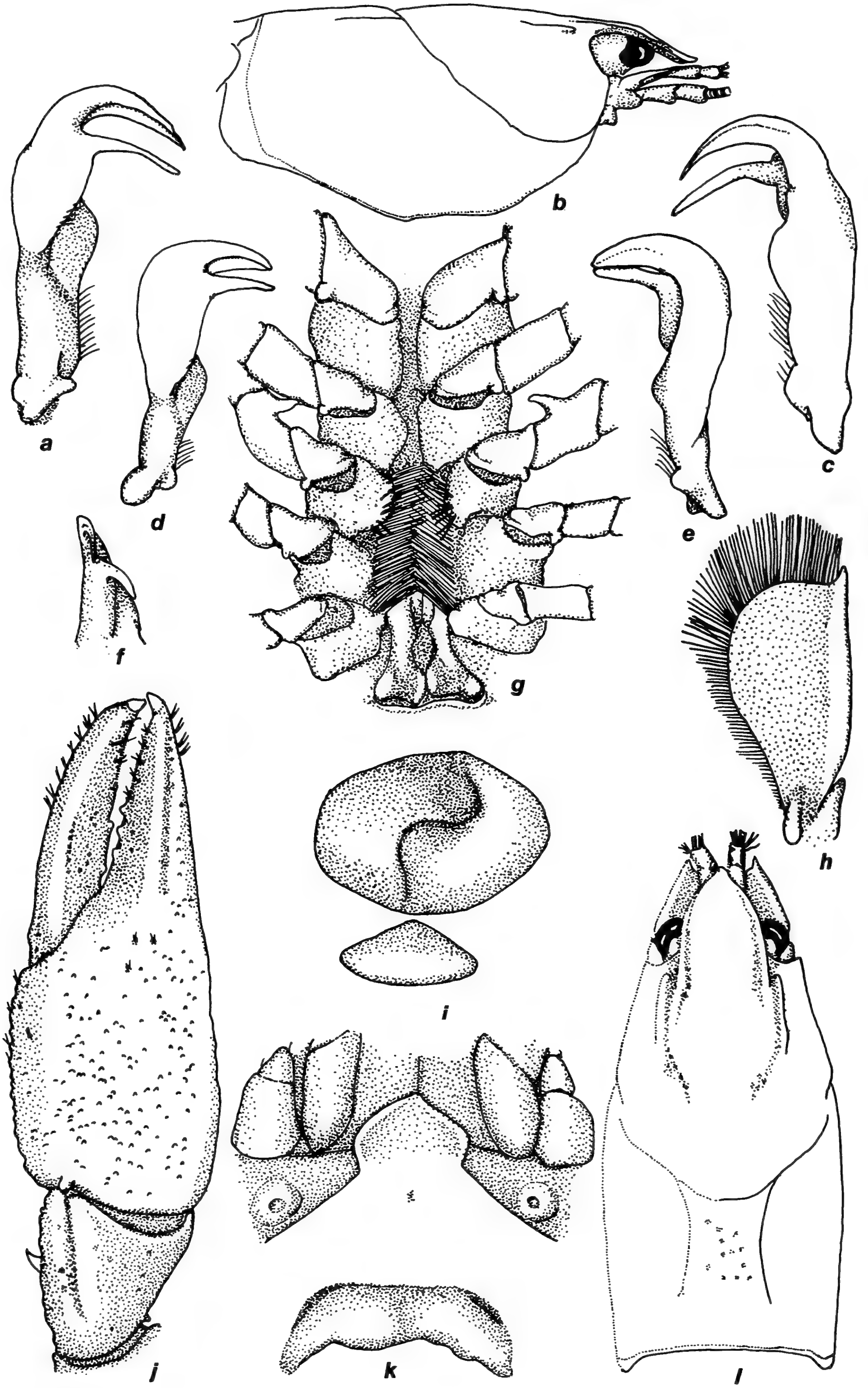
J. F. Fitzpatrick, Jr. and Craig A. Busack

Abstract.—A new crawfish, *Hobbseus yalobushensis,* is described from the headwaters of the Yalobusha River, ultimately a tributary of the Mississippi River. This is the first record of the genus from the Mississippi drainage. The new species is most closely related to *H. prominens* (Hobbs) and *H. petilus* Fitzpatrick. It is distinguished from them by the relative lengths of the terminal elements of the first pleopod of the first form male; females of *H. yalobushensis* are the only members of the genus to have a deep, long trough in the anterior part of the annulus ventralis.

In 1987, one of us (CAB) received a grant from the Mississippi Natural Heritage Program to determine the current status of the rare crawfish *Procambarus* (*Pennides*) *lylei* Fitzpatrick & Hobbs, 1971. During the study, several specimens of a crawfish assignable to the genus *Hobbseus* were collected. These proved to represent an undescribed species and provided the opportunity for the first published record of the genus from the Yalobusha River drainage, and thus, from the Mississippi River basin.

Hobbseus yalobushensis, new species
Fig. 1

Diagnosis.—Pigmented; eyes normal. Rostrum spatulate, without marginal spines; acumen reduced but usually obvious, not sharply delimited basally by strong rostral shoulders. Areola from 34.6 to 41.9% (av. 42.0%) of total carapace length (43.5–51.0%, av. 49.5% of postorbital carapace length) and from 1.75 to 2.73 (av. 2.43) times longer than wide; punctations widely scattered and poorly developed, 2 to 5 across narrowest part. Cervical spines absent. Postorbital ridges strong, terminating cephalically in rounded knob or small tubercle. Branchiostegal spine obsolete; suborbital angle lacking. Antennal scale broadest distal to midlength. Dorsal surface of palm of cheliped studded with squamous tubercles. Ischia of only third pereiopods of males with hooks; bosses lacking on all pereiopodal coxae, but small, sparsely setose, obliquely oriented eminence on caudomesial corner of third, and ventromesial margin of fifth with obvious tubercle bearing one or two long setae. First pleopods of males symmetrical, apices reaching just beyond caudal margin of coxae of third pereiopods and hooded by dense mat of long setae originating mostly from area of lateral margin of sharply arched sternites; terminating in two parts, rami subparallel with apex of each directed at angle of about 115° to main axis of appendage; mesial process only slightly longer than central projection and tapering from base to acute tip; central projection of first form male corneous, with obscure rounded eminence at proximomesial base, and with acute tip. Annulus ventralis movable, subovate in outline; deep, broad trough in cephalic third overhung through most of length of one side by prominent cephalolateral tubercle; sinus, originating in fundus located beneath caudalmost part of aforementioned overhang, moving trans-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versely past midline and then turning sharply caudad following gently undulant path to or nearly to caudal margin. Hand of female sparsely hirsute with comparatively few punctations above and below.

Holotypic male, Form I.—Cephalothorax (Fig. 1*b, l*) subovate, slightly compressed laterally, deeper than wide at level of caudodorsal margin of cervical groove (8.0 and 7.5 mm, respectively). Abdomen longer than carapace (16.0 and 15.4 mm). Areola 2.43 times longer than wide with 3 or 4 irregular rows of poorly delineated punctations, 3 across narrowest part, constituting 36.4% of entire length of carapace (44.1% of postorbital length). Rostrum slightly depressed anteriorly, only weakly excavate dorsally, unthickened elevated margins flanked mesially by deep punctations only near base; acumen slightly upturned, poorly set off from rostrum and not reaching distal margin of penultimate podomere of antennule. Subrostral ridge weak and barely visible in dorsal aspect. Postorbital ridge strong, grooved dorsolaterally, terminating cephalically in rounded, unexpanded knob. Suborbital angle lacking. Branchiostegal spine obsolete. Cervical spine absent; very few deep punctations on carapace, deepest in vague row leading caudomesially from base of postorbital ridge; few low squamous granulations in extreme cephalolateral part.

Cephalic lobe of epistome (Fig. 1*k*) broadly subtriangular, distinctly convex with elevated margins, obtuse fovea in main body. Antennules of usual form with small spine near ventromesial margin of basal article. Antennae extending caudally to midlength of third abdominal tergum; antennal scale (Fig. 1*h*) 1.40 times longer than wide, widest distal to midlength, lateral part thickened, terminating in strong acute spine and overreaching distal margin of ultimate podomere of antennal peduncle.

Cephalic section of telson with single immovable spine in each caudolateral corner and slightly movable spine just mesial to it.

Chela (Fig. 1*j*) somewhat depressed, slightly rotated mesially, subovate in cross section. Upper surface with comparatively prominent tubercles and only sparsely punctate, punctations deep only on fingers and in cluster of three proximal to base of immovable finger. Both fingers with median longitudinal ridge above and below, setiferous punctations more common on dorsal flank of opposable margins. Opposable margin of immovable finger with three prominent tubercles in basal half, single row of minute denticles along distal half. Opposable margin of dactyl with tubercle near midlength and second subequal tubercle near proximal one-tenth, both smaller than tubercles of immovable finger; single row of crowded minute denticles in distal half. Lateral margin of fixed finger with obtuse keel along most of its length and four tufts of setae in distal one-fourth; corresponding margin of palm only slightly undulant; inner margin of palm with single, nearly cristiform row of 13 tubercles, flanked above by three tiny squamous tubercles and, in distal third, below by four. Low but broad squamous tubercle near base of dactyl. Outer margin of dactyl entire with row of submarginal, conspicuously setose punctations in distal half.

Carpus of cheliped slightly longer than wide; dorsal surface with shallow nearly longitudinal furrow toward mesial margin and few scattered setiferous punctations, mostly in distal half; mesial margin with

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Fig. 1. *Hobbseus yalobushensis,* all figures of holotype except *d, e,* morphotypic male; *i,* allotypic female. *a,* Mesial view of first pleopod; *b,* Lateral view of carapace; *c,* Lateral view of first pleopod; *d,* Mesial view of first pleopod; *e,* Lateral view of first pleopod; *f,* Caudal view of tip of first pleopod; *g,* Ventral aspect of basal podomeres of pereiopods; *h,* Antennal scale; *i,* Annulus ventralis; *j,* Dorsal aspect of distal podomeres of cheliped (carpus rotated about 20° laterally to visualize stout mesial spine); *k,* Epistome; *l,* Dorsal view of carapace.

nine irregularly placed squamous to low spiniform tubercles; lower submesial margin with strong, acute spine slightly distal to midlength; lower laterodistal corner with acute spine, lower mesiodistal corner lacking ornamentation. Merus with row of eight subacute spines along ventromesial margin and another of five along ventrolateral margin, with row of four spiniform tubercles on dorsal margin, row terminating in two more small but stout subacute, adjacent spines. Ischium with three small spines along distal two-thirds of mesial margin.

Hooks on ischia of third pereiopods only (Fig. 1*g*); hooks strong, simple, slightly arched, and overhanging basioischial articulation but opposing structure on basis lacking. Coxae of all pereiopods lacking bosses, but third with slightly globose expansion of caudomesial corner bearing irregular arrangement of from seven to nine long, coarse setae; fifth with typical ventromesial setose eminence and penile orifice.

Sternum of third through fifth pereiopods deeply excavate and with dense tufts of setae arising from lateral margins, setae (with minor contributions from proximal parts of coxae) obscuring distal half of pleopods when latter held parallel to body.

First pleopods (Fig. 1*a, c, f*) as described in "Diagnosis"; central projection corneous.

Allotypic female.—Except in secondary sexual characteristics, differing from holotype in following respects: abdomen subequal in length to carapace; mesial margin of palm with row of 12 tubercles; opposable margin of fixed finger with proximalmost tubercle reduced to scarcely more than prominent undulation; mesial margin of carpus with 2 small tubercles and 1 small spine proximal to stout spine, no ornamentation distally; merus with only 3 small spines in ventrolateral row, row ending distally in strong acute spine at corner; ventromesial row of 3 large, 1 small, followed by 3 large, 1 small, and distally, 4 large spines, dorsal surface with 2 spines on distalmost margin.

Annulus ventralis (Fig. 1*i*) movable, subovate in outline, highest (ventrally) just caudal to midlength; deep broad trough arising on cephalomedian margin and progressing obliquely to left of midpoint of annulus, high crescent-shaped eminence (or cephalolateral tubercle) overhanging lateral and caudal extremes of trough; sinus arising in deep fossa located in caudolateral corner of trough, progressing transversely to right of median line, there turning sharply caudad, following gently undulant path to just short of caudal margin. Postannular sclerite prominent, about half width of annulus, and not obscured by caudal margin of latter.

Morphotypic male, Form II.—Differing from holotype in following respects: areola with 4 punctations across narrowest part; proportions of chela more like allotype and inner margin of palm with row of 12 tubercles; mesial surface of carpus with 3 small spines proximal to stout spine, entire dorsally; ventromesial margin of merus with row of 3 large, 1 small, and 3 large spines, lateral row represented by single quite prominent acute spine at base of distal fourth; dorsal surface of same podomere with 3 triangularly arranged stout spines near distal margin.

Both terminal elements of first pleopod (Fig. 1*d, e*) noncorneous, less slender, subequal in length, and apices subacute. Hooks on ischia of third pereiopods conspicuous but markedly less developed, rounded at apex. Left first pleopod with incomplete, obscure suture delimiting basal tenth.

Type locality.—The holotype and allotype were collected from Topashaw Creek, 3.8 airmi. (6.1 km) SW of Mantee (jct. of St. Rtes. 15 and 46), T21N, R11E, at the boundary of Secs. 2 and 11, Webster County, Mississippi. Here the creek flows through agricultural land, but it is shaded by deciduous trees on both banks. The banks have been severely eroded by inflow from two metal culverts draining the fields and located approximately 15 m upstream of the collection site. The creek was from 1 to 2 m wide, and up to 0.7 m deep, with slow flow. The animals were collected by dip net from the streambed of bare mid-phase Porters Creek clay. No plant material other than leaf litter was apparent in the shaded area where the specimens were taken. Other crawfish present were large numbers of an undescribed *Orconectes* species and *Cambarus* (*Depressicambarus*) *striatus* Hay, 1902. The morphotype was taken from Dry Creek, a Topashaw Creek tributary, 0.5 roadmi. (0.8 km) W of Hohenlinden, T15S, R1E, NE/4 SW/4 Sec. 36, also in Webster County.

Disposition of the types.—The holotype, allotype, and morphotype are in the collections of the National Museum of Natural History, Smithsonian Institution (USNM 219513, 219514, and 219515, respectively); the same museum also has three lots of paratypes (1 ♂ I, 5 ♂ II, 2 ♀). Other paratypes are in the collections of the Mississippi Museum of Natural Science, Jackson (MMNS; 4 ♂ I, 5 ♂ II, 5 ♀, 3 ♂ imm., 2 ♀ imm., 12 unsexed imm.); of the Royal Ontario Museum, Toronto (ROM; 1 ♂ I, 1 ♂ II, 1 ♀, 7 ♂ imm., 1 ♀ imm.); and of the Milwaukee Public Museum (MPM; 1 ♂ II, 1 ♀).

Range and specimens examined.—*Hobbseus yalobushensis* has been collected on nine occasions from six localities, all in the headwaters of the Yalobusha River, tributary to the Yazoo River, tributary to the Mississippi River: Calhoun County. (1) Small unmapped tributary of Bear Creek, 7.5 airmi. (12.2 km) SE of Calhoun City (jct. St. Rtes. 8 and 9), T22N, R10E, center Sec. 12, (MMNS; 1 ♀, 1 ♂ imm., 2 ♀ imm.), 13 Feb 1987, C. Busack, M. Belk, and N. Hunt, colls.; Chickasaw County. (2) Topashaw Creek at St. Rte. 340, 4.5 roadmi. (7.3 km) W of St. Rte. 15, T15S, R2E, boundary of Secs. 20 and 21, (ROMIZ 13881; 1 ♂ I, 1 ♂ II, 7 ♂ imm., 1 ♀ imm.), 14 Mar 1988, M. Belk, coll.; (3) Topashaw Creek at St. Rte. 340, 4.5 roadmi. (7.3 km) W of St. Rte. 15, T15S, R2E, boundary of Secs. 20 and 21, (MMNS; 2 ♂ I, 1 ♂ II, 1 ♀, 1 ♂ imm., 1 ♀ imm., 12 unsexed imm.), 26 Mar 1988, C. B. and M. B., colls.; (4) Topashaw Creek at county road, 2.5 roadmi. (4.0 km) W of St. Rte. 341, T15S, R1E, Sec. 23 NW/4, (MMNS; 1 ♂ I, 2 ♂ II, 1 ♀, 1 ♂ imm.), 26 Mar 1988, C. B. and M. B., colls. (5) roadside ditch, 3.4 roadmi. (5.5 km) NW of St. Rte. 9 on St. Rte. 404, (tributary to Sabougla Creek), (USNM 218641; 1 ♂ I), 17 Apr 1967, C. Craig, coll.; (6) 3.4 roadmi. (5.5 km) N of St. Rte. 9 at Bellefontaine on St. Rte. 404, (USNM 207124; 1 ♂ II, 1 ♀), 14 May 1969, T. D. Thornhill, coll.; (7) 3.4 roadmi. (5.5 km) NW of St. Rte. 9 at Bellefontaine on St. Rte. 404, (USNM 207112; 4 ♂ II, 1 ♀), 14 May 1969, C. C., coll.; (8) Dry Creek, 0.5 roadmi. (0.8 km) W of Hohenlinden, R1E, T15S, NE/4 SW/4 Sec. 36, (USNM 219515; 1 ♂ II) (ROMIZ 13882; 1 ♀) (MMNS; 2 ♂ II, 2 ♀) (MPM IZ 1988-30; 1 ♂ II, 1 ♀), 24 Apr 1987, M. B. and K. Baldwin, colls.; (9) type locality, (USNM 219513, 219514; 1 ♂ I, 1 ♀) (MMNS; 1 ♂ I), 5 Jun 1987, C. B. and N. Baldwin, colls. In addition, two immature females collected by C. B., M. B., and C. Hill on 30 Jan 1987 from Sabougla Creek, 1 roadmi. (1.6 km) NW of Bellefontaine, T21N, R9E, SW/4 SE/4 Sec. 24, Webster County, are probably assignable to this species; this collection is at MMNS.

Variations.—Most of the limits of variation seen in this limited number of specimens is reflected in the description of the primary types, above. The second Form I male from the type locality has the apex of the rostrum broadly rounded and is without an acumen; perhaps it was broken early in life; also the mesial margin of the right palm has a row of 15 tubercles. In one of the Form II males (12.5 mm carapace length) collected with the morphotype, the terminal elements of the first pleopod are adpressed throughout their length, and the central projection is markedly the longer element; the pleopod also has a distinct juvenile suture proximally. The rostra of two immature specimens (1 ♂, 1 ♀) have sharply converging margins so that the acumen is acute and clearly delineated.

Size.—The largest animal collected is a

Table 1.—Measurements (in mm) of types of *Hobbseus yalobushensis*.

	Holotype	Allotype	Morphotype
Carapace			
Total length	15.4	16.5	14.1
Postorbital length	12.7	13.2	11.5
Width	7.5	8.0	7.0
Height	8.0	8.6	7.4
Areola			
Length	5.6	5.8	5.1
Width	2.3	2.2	2.1
Antennal scale			
Length	3.5	3.6	3.4
Width	2.5	2.5	2.5
Rostrum			
Length	6.2	6.6	5.5
Width	4.2	4.1	3.9
Chela			
Length, mesial margin palm	4.6	5.0*	4.0
Width, palm	4.6	4.5*	4.0
Length, lateral margin propodus	9.6	8.8*	7.4
Length, dactyl	5.5	5.4*	4.8
Abdomen			
Length	16.0	16.5	15.4
Width	6.5	7.7	6.4

* Left chela; right regenerated.

female 21.8 mm in cephalothorax length. The largest first form male is 18.0 mm, and the smallest 14.8 mm. No ovigerous females or females carrying young were collected. For measurements of the primary types see Table 1.

Color notes.—The color patterns are extremely variable, ranging from medium brown with frequent irregular black splotches dorsally, and becoming nearly concolorous black laterally, to uniform medium tan, except for two poorly defined dorsolaterally placed dark lines extending from the mid-cephalic area to the cephalic margin of the telson. The abdomen is pale brown dorsally, except for the aforementioned lines which degenerate to a series of irregular splotches at the tergal margins. A dark reddish brown line marks the boundary between pleura and terga. The dorsal surface of the chela is basically orange brown, deepening to very dark brown on the fingers. The fingers are nearly white at the tips. The carpus, except for a light oblique groove, and the merus of the cheliped are dark brown dorsally. The pereiopods are dark brown dorsally and distally, fading to pink ventrally and proximally. The undersides of the abdomen and cephalothorax are white; those of the proximal pereiopodal segments are white but deepen to pink at the ischia or meropodites. A varying intensity of pink coloration imparts a striped appearance to the pereiopods, especially in juveniles.

Associates.—*H. yalobushensis* has been collected in association with *Cambarus* (*Depressicambarus*) *striatus, Procambarus* (*Ortmannicus*) *hayi* (Faxon, 1884), *Procambarus* (*Pennides*) *vioscai* Penn, 1946, and an undescribed species of *Orconectes.*

Relationships.—The nearest relatives of *Hobbseus yalobushensis* are *H. prominens* (Hobbs, 1966) and *H. petilus* Fitzpatrick, 1977. It can be distinguished from the former by its less spatulate rostrum and that in *H. prominens* the terminal elements are slightly divergent. In both of the previously described species the mesial process is markedly longer than the central projection; the mesial process is, at best, only slightly longer in *H. yalobushensis. Hobbseus yalobushensis* is unique in the genus in having such a well-developed, broad, long trough in the annulus ventralis and in having comparatively heavy, non-uniform tuberculate ornamentation on the dorsal surface of the palm of the chela.

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HIPPOLYTE ZOSTERICOLA (CRUSTACEA: DECAPODA) IN THE EASTERN PACIFIC

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Abstract.—Specimens of *Hippolyte zostericola* have been taken in western Colombia. These animals fall well within the range of variation found in specimens from the Atlantic and Caribbean regions, and can be distinguished readily from *H. williamsi,* the other common hippolytid shrimp of the tropical eastern Pacific.

During a survey of caridean shrimp of western Colombia, Gabriel Ramos of the Universidad del Valle sent me 18 specimens of an unidentified hippolytid shrimp, taken at San Antonio, Municipio de Robles, Tumaco (about 2°N, 79°W), on a mud bottom, 3 Aug 1984, by Henry von Prohl. All but one were ovigerous females, no functional males were collected. The shrimp fall within the range of variation for *Hippolyte zostericola* (Smith), previously reported from Massachusetts, U.S.A. to Yucatan, the Bermudas, and south to Trinidad, Curaçao, and Ceara, Brazil (Chace 1972, Williams 1984). The specimens from Colombia have been placed in the collections of the National Museum of Natural History, Smithsonian Institution, and the Allan Hancock Foundation, University of Southern California and Los Angeles County Museum of Natural History. Another five specimens, examined by Gabriel Ramos, have been added to the collections of the Universidad del Valle in Cali, Colombia (catalog number CRBMUV 84013).

Hippolyte zostericola is variable: the rostrum usually overreaches the antennular peduncle in adult females, and bears from one to three dorsal and from one to four ventral teeth. The basal article of the antennular peduncle is long and broad, without terminal spines. The rostrum is slightly shorter than the blade of the antennal scale. The third pereopod has a stout dactyl armed with three large, terminal spines grading into a series of smaller spines on the flexor margin. There is only one spine on the carpus and merus of the third pereopod.

Chace (1972) and Williams (1984) remarked on the similarity between *H. zostericola* and *H. pleuracanthus* (Stimpson), reported from Connecticut to North Carolina. The latter species has a shorter rostrum, not overreaching the antennular peduncle, with from one to three dorsal and from one to three ventral teeth. Chace (Fig. 48) shows *H. pleuracanthus* as having a rostrum terminating in a sharp point, with two ventral subterminal teeth close to the tip, while *H. zostericola* is shown as having a rostrum with a nearly bifurcate tip and two ventral teeth well removed from the tip. *H. pleuracanthus* is shown having four spines on the merus of the third pereopod. Specimens of *H. zostericola* from the Gulf of Mexico tend to have the longest rostrum within the species, while some from Massachusetts have a rostrum not exceeding the antennular peduncle.

The specimens from western Colombia vary considerably. All but two have a rostrum barely exceeding the antennular peduncle, with two or three dorsal and two ventral teeth and a bifurcate tip. In two, the rostrum is shorter than the antennular peduncle, barely exceeding the cornea of the eye. One has one dorsal and one ventral tooth, while the other has two dorsal teeth and a single apical point, not a bifurcate tip. As in *H. zostericola,* the basal segment of the antennular peduncle lacks spines, and the merus of the third pereopod bears one spine. The dactyls are similar in both species.

I compared the specimens from Colombia with individuals of *H. zostericola* from Redfish Bay, Texas. In the latter specimens, the rostrum exceeded the antennular peduncle, and had two dorsal and three ventral teeth with a bifurcate tip. Except that the rostrum was proportionally longer, the specimens were similar.

One cannot rule out the possibility that the specimens from Colombia, isolated from populations in the western Atlantic and Caribbean, belong to a distinct species. Geminate pairs of species living on opposite sides of the Panamic land mass are known among other decapods, such as the spider crabs *Pelia pacifica* (Pacific) and *P. mutica* (Atlantic and Caribbean) and many others (Garth 1958). Although the specimens from the eastern Pacific are indistinguishable from *H. zostericola* on the basis of morphology, there may be genetic, behavioral or ecological differences that warrant their future designation as a separate species.

One other species of *Hippolyte, H. williamsi* Schmitt, can be common in the tropical eastern Pacific. It is readily distinguishable from *H. zostericola* by the presence of three spines on the basal segment of the antennular peduncle. Mature females are about 25 mm in total length, while the largest adult *H. zostericola* from Colombia is 10.7 mm long. Williams (1984) gives a total length of 15.5 mm for females of *H. zostericola.* In *H. williamsi,* the rostrum of the female greatly exceeds the antennular peduncle. The two species may differ in habitat; *H. zostericola* lives among sea grasses and in sheltered bays, while *H. williamsi* can be common in tidepools and rocky areas with algae.

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CHACEON RAMOSAE, A NEW DEEP-WATER CRAB FROM BRAZIL (CRUSTACEA: DECAPODA: GERYONIDAE)

Raymond B. Manning, Marcos Siqueira Tavares, and
Elaine Figueiredo Albuquerque

Abstract.—*Chaceon ramosae,* a species with depressed dactyli on the walking legs previously identified with *C. quinquedens* (Smith, 1879), is described as new, based upon material from Brazil.

Almost no attempt has been made to study the deep-water fauna off the Brazilian coast since the *Challenger* Expedition (1873–1876). Collections made by subsequent oceanographic expeditions such as those carried out aboard the *Albatross* in 1887 and the *Calypso* (1961–1962) were largely restricted to areas of the Brazilian continental shelf. Information on the Brazilian deep-water decapod crustaceans is scarce and is largely confined to studies by Miers (1886), Bate (1888), Henderson (1888) (all based on the *Challenger* collections), Moreira (1901), and Rathbun (1937).

Knowledge of the deep-water species of Brazil has been broadened as a result of the cruise in 1987 of the *Marion Dufresne,* an oceanographic ship of the TAAF (Terres Australes et Antarctique Françaises). The cruise was conducted off southeastern Brazil (Fig. 1) as part of a formal agreement between the Muséum National d'Histoire Naturelle, Paris, and the Universidade Santa Ursula, Rio de Janeiro. Among the materials collected were four large specimens of the deep-sea crab genus *Chaceon* which proved to represent an undescribed species. That species is named below.

The holotype has been deposited in the Museu Nacional, Rio de Janeiro (MNRJ). Other specimens, all paratypes, are in the collections of the Museu de Zoologia, Universidade de São Paulo (MZUSP), the Muséum National d'Histoire Naturelle, Paris (MNHN), and the National Museum of Natural History, Smithsonian Institution, Washington (USNM).

The following abbreviations are used below: cb, carapace width (including lateral spines); cl, carapace length, along midline; fm, fathoms; m, meters; mm, millimeters.

Chaceon ramosae, new species
Figs. 2–3

Geryon quinquedens.—Rathbun, 1937:270, 271 [part, specimen from Brazil only].—Scelzo & Valentini, 1974:561 [part, specimens from Brazil only]. [Not *Geryon quinquedens* Smith, 1879.]

Previous records.—Brazil: 24°17′S, 42°48′30″W, 671 fm (1228 m) (Rathbun 1937).—24°28′S, 43°43′W, 800 m, and 25°13′S, 44°33′W, 1200 m (Scelzo & Valentini 1974).

Material.—Brazil: 19°38′S, 38°43′W, 960 m, sta. 55 CB 95, 30 May 1987: 1 male (MZUSP 9363).—21°31′S, 40°07′W, 750–785 m, sta. 4 CP 7, 10 May 1987: 1 male (holotype, MNRJ-MD-1381).—23°46′S, 42°09′W, 592–610 m, sta. 64 CB 105, 2 Jun 1987: 2 males (MNRJ-MD-1382; MNHN).—24°17′S, 42°48′30″W, 671 fm (1228 m), *Albatross* sta. 2763, 31 Dec 1887: 1 male (USNM 22072).

Description.—A large *Chaceon,* cl to 143 mm, cb to 158 mm in adults, with 5 anterolateral teeth on the carapace and dorsoventrally depressed dactyli on the walking

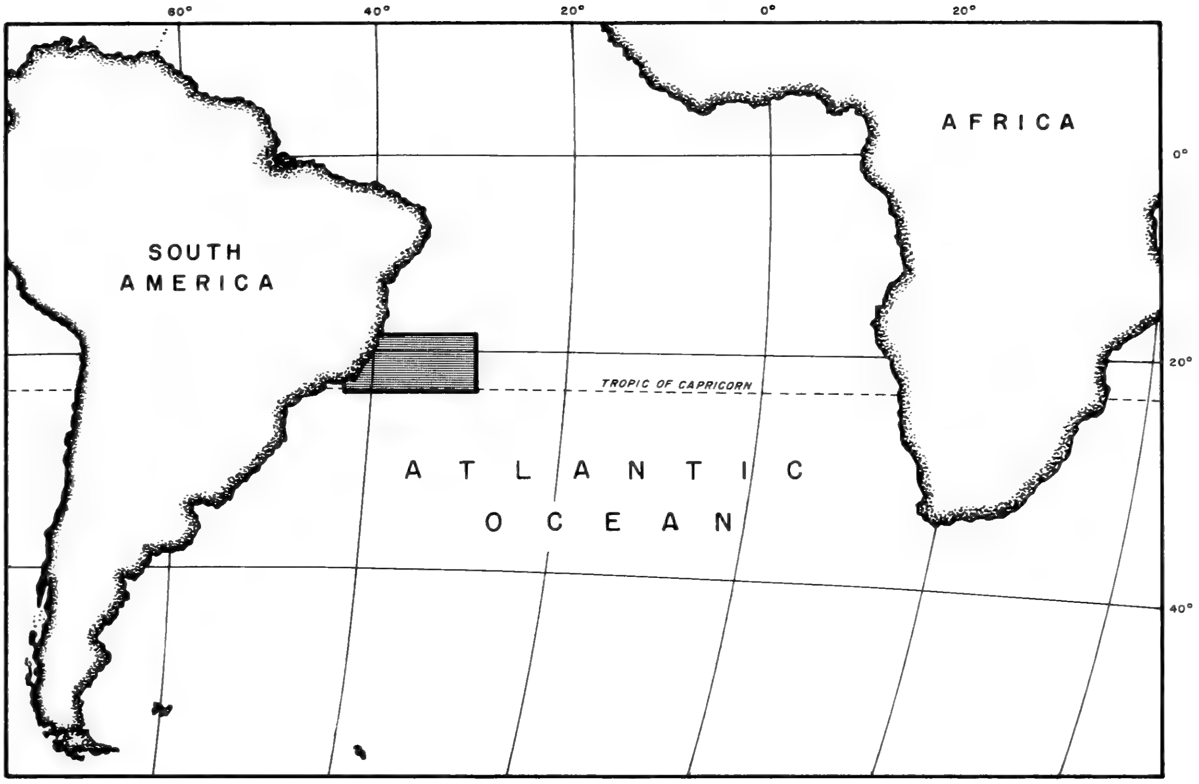

Fig. 1. Area sampled by the *Marion Dufresne* in 1987.

legs. Carapace 1.1 to 1.2 times broader than long. Median pair of frontal teeth separated by U-shaped sinus. Distance between submedian frontal teeth less than distance between them and lateral frontal teeth. Second, third, and fourth anterolateral teeth obsolete in adults, second and fourth smallest of all; distance from first to third tooth less than that from third to fifth tooth. Carapace with distinct raised ridge mesial to fifth anterolateral tooth, carapace surface finely granular, especially posterolaterally, smooth only at hepatic regions. Suborbital tooth short and broad in adults, not extending to level of lateral frontal teeth. Cheliped merus with sharp tooth subdistally, lacking distal tooth or angled lobe; carpus roughened dorsally, usually with irregular, curved granular ridge extending from middle of proximal margin to inner spine, anterior margin of carpus with at most an angled lobe but no spine; propodus with at most distal angled projection dorsally. Meri of walking legs with at most indistinct distal, dorsal tooth. Dactyli of walking legs depressed, height at midlength less than width. Fifth leg: merus usually less than 5.0 times (range 4.6–4.9 in adults, 6.4 in juvenile male) times longer than high, length 0.65 to 0.66 cb in adult; carpus with line of sharp granules dorsally; propodus length 4.1 to 4.3 times height in adult, 5.1 times height in juvenile, longer than dactylus.

Size.—Males only known, cl 28 to 127 mm, cb 36 to 146 mm in material examined. Rathbun's specimen is the smallest specimen reported here. Scelzo & Valentini (1974) studied two males with cl 133 to 143 mm, cb 146 to 158 mm.

Color.—The specimens taken by the *Marion Dufresne* were cream colored in life. Scelzo & Valentini (1974) reported that the color of their two specimens was "cremoso."

Depth range.—Our specimens were taken in depths between 601 (592–610) and 1228 meters, with all records from depths in excess of 600 meters. Scelzo & Valentini (1974) reported two specimens from 800 m and 1200 m. The smallest specimen studied, a male with cl 28 mm, came from 1228 meters.

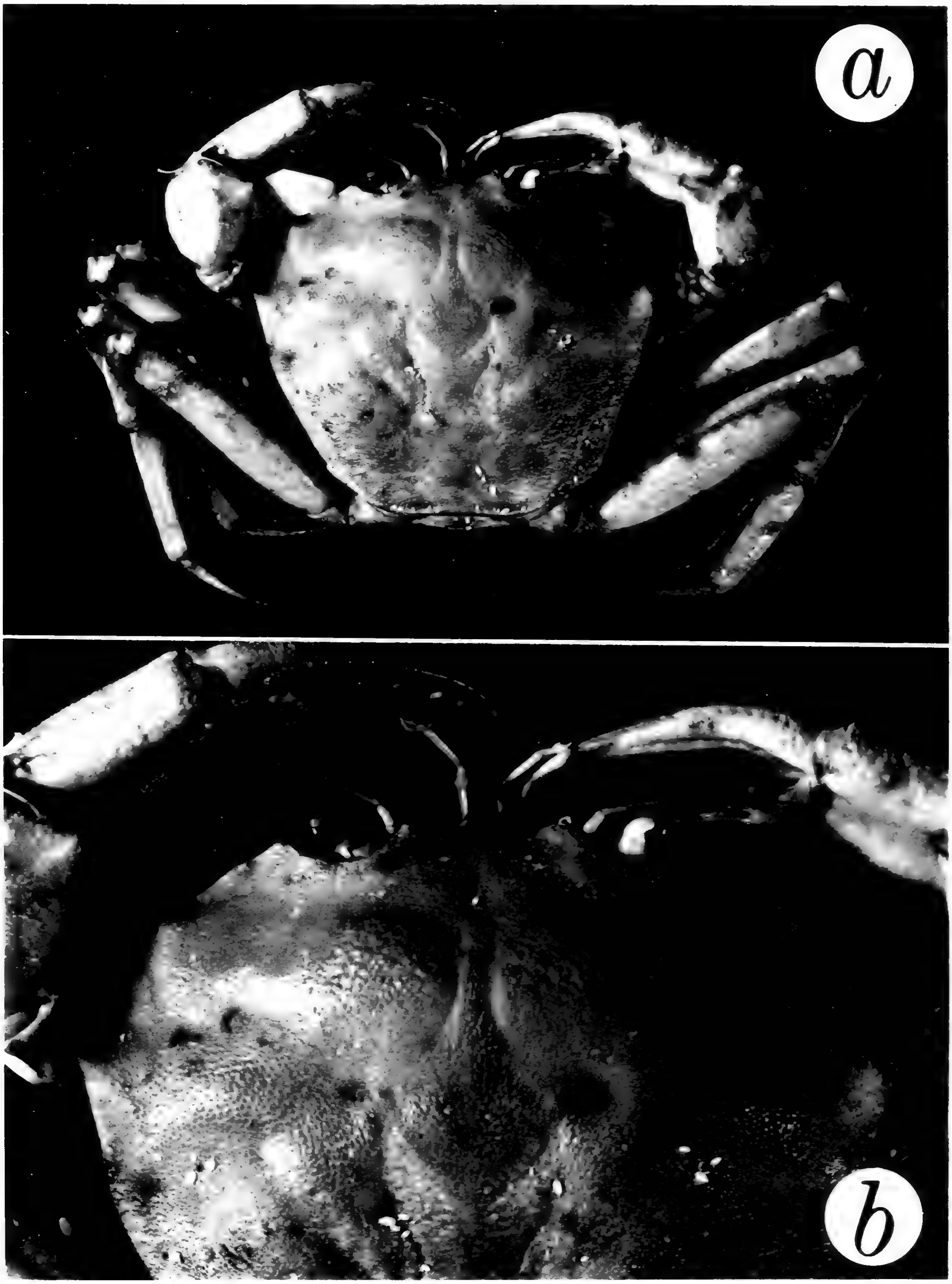

Fig. 2. *Chaceon ramosae,* male paratype, cl 107 mm, sta. 64 CB 105: *a,* Dorsal view; *b,* Carapace.

Remarks.—This species resembles *C. quinquedens* (Smith, 1879) in having depressed dactyli on the walking legs, but differs in numerous features: the carapace is much more granular posterolaterally, the suborbital tooth is less developed, the carpus of the chela completely lacks an outer spine in adults, the propodus of the chela lacks a distal dorsal spine, the meri of the walking legs lack a distinct distal dorsal spine, and the propodus of the fifth leg is less than 5 times as long as high.

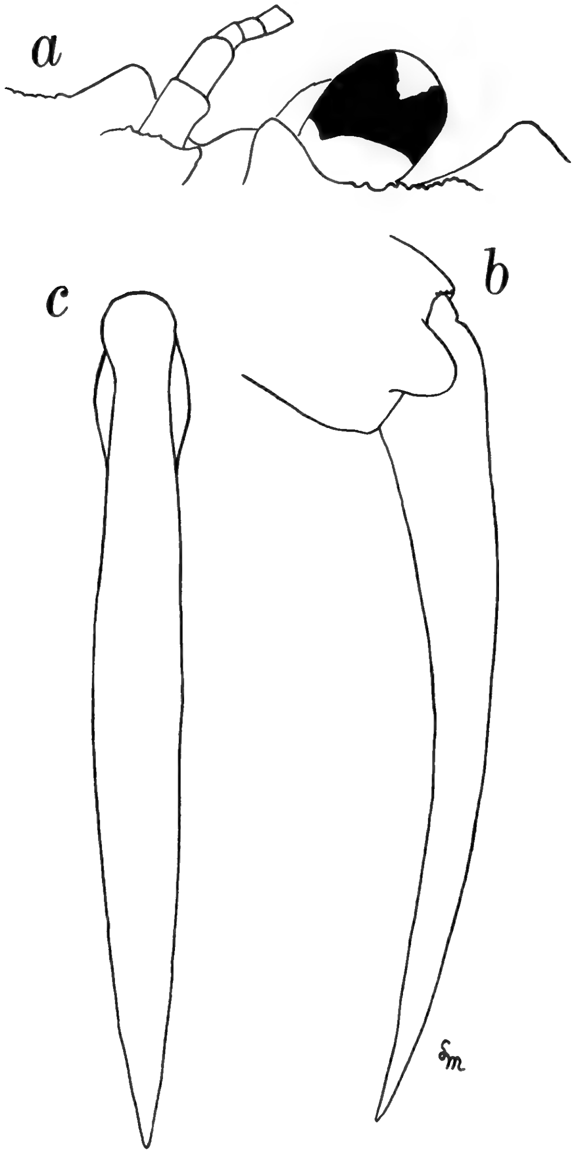

Fig. 3. *Chaceon ramosae,* male paratype, cl 107 mm, sta. 64 CB 105: *a,* Suborbital margin; *b,* Dactylus of fifth leg, posterior view; *c,* Dactylus of fifth leg, dorsal view.

Chaceon maritae (Manning & Holthuis, 1981), from West Africa, also has depressed dactyli on the walking legs, but differs from *C. ramosae* in several features: the carapace granulation is much coarser, the suborbital spine is smaller, and the walking legs are shorter. The merus and propodus of the fifth leg are about 4 times as long as high.

The anterolateral spines of the carapace are more distinct in the smallest specimen; in very large specimens the second and fourth teeth are scarcely discernible, and the third tooth is very low, an obtuse lobe. The merus of the fifth leg is more than 6 times longer than high only in the smallest specimen, cl 28 mm.

Scelzo & Valentini (1974) reported two specimens taken off Brazil in addition to numerous specimens taken off Uruguay and Argentina. Their material from Brazil differed from the other specimens they identified as *Geryon quinquedens* in being cream rather than reddish in color, and in the length/height ratios of the propodi of the walking legs, 4.3 to 4.5, which is similar to our findings. Their material from south of Brazil has been referred to *C. notialis* Manning & Holthuis (1989), who also transferred all large geryonids with 5 anterolateral spines on the carapace to the genus *Chaceon* Manning & Holthuis (1989).

Etymology.—We take pleasure in naming this species for Jeanete Maron Ramos, Universidade Santa Ursula, one of the organizers of the cruise of the *Marion Dufresne* off the Brazilian coast.

Acknowledgments

We thank Alain Guille, Muséum National d'Histoire Naturelle, Paris, and Janete Maron Ramos, Universidade Santa Ursula, for making available the material of *C. ramosae.* Enrique Macpherson of the Instituto de Ciencias del Mar in Barcelona informed one of us (RBM) of the *Chaceon* taken by the French-Brazilian expedition, and he is responsible for our establishing contact. The photographs were taken by Roy Kropp and Marilyn Schotte. Lilly King Manning made the line drawings, and prepared all of the figures for publication.

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ON THE CRAYFISH GENUS *FALLICAMBARUS* (DECAPODA: CAMBARIDAE) IN ARKANSAS, WITH NOTES ON THE *FODIENS* COMPLEX AND DESCRIPTIONS OF TWO NEW SPECIES

Horton H. Hobbs, Jr. and Henry W. Robison

Abstract.—The genus *Fallicambarus,* embracing 16 species of burrowing crayfishes, is represented in Arkansas by eight of them, five of which are members of the nominate subgenus and three assigned to the subgenus *Creaserinus.* A key is provided for the identification of the 16, the combined ranges of which extend from Ontario to southwestern Texas and southwestern Georgia, and from South Carolina to Maryland. *Fallicambarus* (*F.*) *petilicarpus,* a close relative of *F.* (*F.*) *dissitus,* is described from Union County, Arkansas, and *F.* (*C.*) *gilpini,* related to *F.* (*C.*) *caesius,* from Jefferson County, Arkansas. Data are presented for placing *Fallicambarus* (*C.*) *uhleri* (Faxon) and *F.* (*C.*) *hedgpethi* (Hobbs) in the synonymy of *F.* (*C.*) *fodiens* (Cottle). For each of the species occurring in Arkansas, as a complete a synonymy as possible is offered along with a diagnosis of the species; also included are a statement of the range, a list of localities (also noted on spot maps) and specimens examined, color notes, size ranges of adults, and life history and ecological notes.

Among the more interesting and least known of the crayfishes of Arkansas are eight species assigned to the genus *Fallicambarus.* Like all of their congeners, those occurring in Arkansas are seldom found in permanent bodies of water, and, as adults, only after rains or during floods do they frequent temporary pools or runoff. Throughout most of their lives, these crayfishes inhabit burrows that are excavated in areas where, for most of the year, the water table does not drop more than a meter or so beneath the surface (in Arkansas, such areas exposed to the sun often may be recognized by the presence of hydrophilic sedges). Turrets, sometimes in the form of slender chimneys, but more often irregular mounds of earthen pellets of a size proportional to that of the crayfish, mark the scattered burrows which, in many areas, may be seen in, or adjacent to, roadside ditches. Less frequently, clusters of mounds, or even entire fields studded with turrets signify the presence of large colonies of these crayfishes.

Although seldom seen during daylight hours, on warm evenings individuals, with chelipeds extended, may be observed at the mouths of their lairs, sometimes perched at the top of a chimney, or, when the humidity is sufficiently high, and particularly following a shower, walking over the ground. During the early spring and after rains, evidence of the presence of a crayfish in its domocile is provided by damp-to-wet pellets of soil recently deposited at openings to the burrows. Such signs of recent excavation are seen most frequently early in the day, before the pellets have become dry, but, if the weather is overcast, recent deposits may be found at almost any hour.

At one time or another, there exist for most burrows constructed by members of the genus *Fallicambarus* more than one opening at the surface that lead into the simple or complex system of galleries. The simplest burrows constructed by these crayfishes in Arkansas are those of *F.* (*C.*) *fodiens* (Cottle, 1863). Often they consist of a single subvertical tunnel with a slight enlargement at the fundus, but more often they are made more complex by the addition of a side passage leading to or toward the surface, and on rare occasions, when a second adult shares the domicile with an ovigerous female or one bearing young, there may exist a secondary gallery leading downward. Thus in its simplest form, the burrow consists of passages that are subvertical and are disposed in the forms of an "I," "Y" (sometimes inverted), or "X." The more complex patterns usually occur in areas where during much of the year the water table lies very near or almost at the surface. The galleries of these burrows are disposed largely subparallel to the surface, and except for one or two that descend, presumably to the maximum depth to which the water table drops, lie relatively close to the surface. Usually there are at least two exits, one of them nearly always topped by a turret that is sometimes open, but during dry weather may not only be closed but also the passage leading to it is often "back-filled." If the burrow is that of an ovigerous female or one carrying young, all openings to the surface are frequently plugged. During wet seasons, all of the galleries may be water-filled, but at other times water may be found only at the bottom of the one or two deep passages. A few burrows have been excavated in which no standing water was present.

The range of the genus *Fallicambarus* is a discontinuous one in which the larger segment extends from Ontario southward to Arkansas County, Texas, and eastward to the Apalachicola River basin of southwestern Georgia. The more eastern segment encompasses the Coastal Plain and lower Piedmont provinces from New Jersey to South Carolina. In Arkansas, the genus is confined to the Coastal Plain and foothills of the Ozark and Ouachita mountains. There the nominate subgenus, which is not known to occur east of the Ouachita River basin in Arkansas and Louisiana or west of the Brazos Basin in Texas, is restricted to the Ouachita and Red river basins. The much more widespread subgenus *Creaserinus,* however, occurs in all of the major drainage basins in the state, overlapping much of the range of the subgenus *Fallicambarus.*

Of the eight species present in Arkansas, five are members of the nominate subgenus: *Fallicambarus* (*F.*) *dissitus* (Penn, 1955), *F.* (*F.*) *harpi* Hobbs & Robison (1985), *F.* (*F.*) *jeanae* Hobbs (1973), *F.* (*F.*) *petilicarpus,* new species, and *F.* (*F.*) *strawni* (Reimer, 1966); and three are assigned to the subgenus *Creaserinus*: *F.* (*C.*) *caesius* Hobbs (1975), *F.* (*C.*) *fodiens* Cottle (1863), and *F.* (*C.*) *gilpini,* new species. Little is known about any of them except *F.* (*C.*) *fodiens,* and no investigation has involved a comparison of representatives of populations throughout the range of the species. Moreover, considerations of its relationship to *F.* (*C.*) *uhleri* and *F.* (*C.*) *hedgpethi* have been only cursory, the principal reason being a lack of specimens from much of the suspected or assumed ranges of the three species. In many, if not most, of the collections that were available, there were no first form males. The latter problem persists to date, for in less than half of the collections that we have examined is even one such specimen present. As a result we cannot be confident that the one or two males in a collection exhibit secondary sexual characters, the most useful that we have encountered, that are typical of the local population. In defense of the conclusions offered, however, we point out that such features appear to be remarkably uniform in the first form males in most localities represented in our material by two or more such males. This observation has prompted the question as to why so few of these males have been collected.

The following represents primarily an account of our knowledge of the genus *Falli-*

cambarus in Arkansas, although we have attempted to summarize all available data on those species that range beyond the state boundaries. Indeed, the diversity noted in the populations of *F.* (*F.*) *fodiens* occurring in Arkansas provoked us into a study of representatives of the species throughout its range, one of the largest of any crayfish in North America. In presenting the synonymies, diagnoses, bibliographic references, and summaries of published biological data for each of the species occurring in the state, we have included all of which we are aware, and the following key encompasses all of the species that have been assigned to the genus.

Abbreviations used herein are as follows: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; cl, carapace length; CM, Carnegie Museum, Pittsburgh; pol, postorbital carapace length; TU, Tulane University, New Orleans; USNM, National Museum of Natural History, Smithsonian Institution.

Genus *Fallicambarus* Hobbs (1969a)

Diagnosis.—"Adults with rostrum devoid of marginal spines. Mesial margin of palm of chela with row of fewer than 12 tubercles, opposable margin of dactyl usually with prominent excision. Areola linear or obliterated [along part of its length]. Antennal scale more than twice as long as broad. First pleopods of first form male symmetrical and terminating in two or three distinct parts (mesial process, central projection and, occasionally, cephalic process; caudal element always absent) bent caudally or caudomesially at angle of 90 degrees or more to main shaft or forming broad arc; central projection corneous, blade-like or tapering (but flattened laterally) and [frequently] lacking . . . subapical notch; non-corneous mesial process never bulbiform but often appearing twisted and usually with eminence on cephalic (morphological) border slightly distal to base; cephalic process, when present, small, at least partially corneous, situated mesially at base of mesial process, and directed caudally or caudodistally" (slightly modified from Hobbs 1973:463). Type species: *Cambarus strawni* Reimer, 1966:11. Gender: masculine.

This taxon was proposed by Hobbs (1969a:111) to receive an assemblage of eight species that had been assigned formerly to the genus *Cambarus*. Subsequently, the diagnosis of this assemblage was revised by him (1973:462), and speculations were offered on the interrelationships of the 11 members recognized at the time. In pointing out more formally the existence of two species groups among these crayfishes, he proposed the adoption of two subgenera: the nominate subgenus comprising five species, and the subgenus *Creaserinus,* six. In this summary the former subgenus is considered to consist of seven species, two of which have been described since 1973 and one herein; *F.* (*F.*) *spectrum* has been relegated to the synonymy of *F.* (*F.*) *jeanae* (Hobbs 1989). The subgenus *Creaserinus* as presently constituted consists of nine species, four of which were described since 1973 and one is added in this study. Evidence for placing *Fallicambarus* (*C.*) *hedgpethi* and *F.* (*C.*) *uhleri* in synonymy with *F.* (*C.*) *fodiens* is detailed herein.

Key to Species of Genus *Fallicambarus* (Based on First Form Males)

1\. First pleopod with proximomesial spur (Fig. 3*i*) . . . . . (Subgenus *Fallicambarus*) . 2

1′. First pleopod lacking proximomesial spur (Fig. 11*h*) . . . . . .(Subgenus *Creaserinus*) . . 8

2\. Mesial ramus of uropod with distinct distolateral spine (Fig. 1*c*); abdomen not conspicuously narrower than thorax . 3

2′. Mesial ramus of uropod lacking distinct distolateral spine

(Fig. 1*d*); abdomen conspicuously narrower than thorax . 5

3. Mesial ramus of uropod with distomedian spine projecting beyond margin of ramus (Fig. 1*c*); cheliped with sufflamen (Fig. 10*z*); central projection disposed proximocaudally, never overlapping that of corresponding pleopod (Fig. 11*h*) .... *macneesei*

3′. Mesial ramus of uropod with distomedian spine never projecting beyond margin of ramus (Fig. 11*d*); cheliped without sufflamen (Fig. 10*a*′); central projection disposed proximomesially, its distal extremity frequently overlapping that of corresponding pleopod (Fig. 3*i*) 4

4(3′). First pleopod with cephalic process (Fig. 3*b*); length of carpus of cheliped distinctly greater than width of palm of chela (Fig. 3*h*) ...... *petilicarpus*

4′. First pleopod lacking cephalic process (Fig. 1*e*); length of carpus of cheliped subequal to or less than width of palm of chela .... *dissitus*

5(2′). First pleopod without cephalic process (Fig. 1*f*) .... *jeanae*

5′. First pleopod with cephalic process (like Fig. 1*g*) 6

6(5′). Ischia of third and fourth pereiopods with hooks (like Fig. 3*n*) .... *devastator*

6′. Ischia of third pereiopods only with hooks (like Fig. 11*m*) .. 7

7(6′). Cephalic process of first pleopod extending caudodistally (Fig. 1*g*); mesial ramus of uropod without distomedian spine (like Fig. 1*d*) .... *harpi*

7′. Cephalic process of first pleopod closely paralleling basal part of mesial process (Fig. 10*y*), apical part if free directed caudally; mesial ramus of uropod with distomedian premarginal spine .... *strawni*

8(1′). Ventral surface of merus of cheliped with one row of tubercles (Fig. 1*q*) 9

8′. Ventral surface of merus of cheliped with two rows of tubercles (Fig. 1*p*) 10

9(8). Mesial surface of dactyl of chela with tubercles in basal half (Fig. 1*r*); mesial ramus of uropod lacking distolateral spine .... *caesius*

9′. Mesial surface of dactyl of chela lacking tubercles (Fig. 11*o*); mesial ramus of uropod with distolateral spine (Fig. 11*d*) .... *gilpini*

10(8′). Mesial surface of palm of chela of second pereiopod not bearded (Fig. 1*a*); shaft of first pleopod strongly reflexed (Fig. 1*h, j*) 11

10′. Mesial surface of palm of chela of second pereiopod bearded (Fig. 1*b*); shaft of first pleopod straight or only slightly curved (Figs. 1*i, k, l,* 8, 9, 10*a–x* 13

11(10). First pleopod with central projection not conspicuously long and slender (Fig. 1*h*) *byersi*

11′. First pleopod with central projection conspicuously long and slender (Fig. 1*j*) 12

12(11′). Antennal scale tapering distally to strong distolateral spine (Fig. 1*n*); boss on coxa of fourth pereiopod ridgelike (Fig. 10*c*′) .... *gordoni*

12′. Antennal scale rounded to subtruncate distally, lacking distolateral spine (Fig. 1*m*); boss on coxa of fourth pereiopod bulbiform (10*b*′) ..... *burrisi*

13(10′). First pleopod with central projection straight and truncate distally (Fig. 1*i*) .... *hortoni*

13′. First pleopod with central projection arched, and tapering at distal extremity or bearing subapical notch (Figs. 1*k*, *l*, 8, 9, 10*a–x* 14

14(13′). Antennal scale with somewhat distinct distal and mesial margins, their junction subangular (Fig. 1*o*); abdomen broadly joined to cephalothorax .... *fodiens*

14′. Antennal scale with distomesial margin strongly inclined abdomen narrowly joined to thorax 15

15(14′). First pleopod with mesial process conspicuously overreaching central projection (Fig. 1*k*) .... *danielae*

15′. First pleopod with mesial process overreaching central projection little if any (Fig. 1*l*) . ... *oryktes*

Subgenus *Fallicambarus* Hobbs (1973)

Diagnosis.—First pleopod of male with proximomesial spur and sometimes with cephalic process. Cheliped without sufflamen, except in *F. macneesei,* chela with tubercles scattered over most of dorsal surface, lateral margin of palm and basal part of fixed finger rounded, more often subserrate or serrate, never smoothly costate. Second pereiopod of male with mesial face of chela and carpus lacking dense mats of plumose setae. Coxa of fourth pereiopod usually with conspicuously large boss.

Fallicambarus (*Fallicambarus*) *dissitus*
(Penn)
Figs. 1*e,* 2

Cambarus dissitus (Penn, 1955:73–80, figs. 1–13 [Types: holotype, allotype, and morphotype, USNM 98125, 98126, 98127; paratypes, ANSP, AMNH, CM, TU, USNM. Type locality: three miles east of Choudrant, Lincoln Parish, Louisiana.]; 1959:5, 6, 9, 11, 15, 16, 17, figs. 25, 48, 66, 79.—Penn & Marlow, 1959: 202.—Hobbs, 1959:896; 1962:274; 1967: 13.—Black, 1967:173, 178.—Fitzpatrick & Payne, 1968:14.—Hobbs III, 1969:19, 21, tab. 2.

Fallicambarus dissitus.—Hobbs, 1969a:111, 124, 173, fig. 20d; 1972:15, 99, figs. 81c, 82d; 1974b:23, 102, fig. 88.—Feinberg, 1971:26.—Hart & Hart, 1974:26, 30.—Bouchard, 1978:432; 1980:432.—Bouchard & Robison, 1981:26, 29.

Fallicambarus (*Fallicambarus*) *dissitus.*—Hobbs, 1973:463, 477–479, fig. 4.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:167.—Hobbs & Robison, 1985: 1035.

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subsequal to, width of palm of chela. Chela with lateral margin at least weakly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles along at least proximal fourth. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, lacking cephalic process; central projection strongly arched, inclined laterally at base, its distal part directed proximomesially and often crossing that of corresponding pleopod. Hooks on ischia of third and fourth pereiopods. Boss on coxa of fourth pereiopod moderately strong and compressed. Mesial ramus of uropod with distolateral and distomedian spine, latter premarginal. Telson divided and with spine/s flanking anterolateral flank of suture.

Range and specimens examined.—This crayfish is known from only a few localities in the Red and Ouachita river basins of southern Arkansas (Columbia County) and

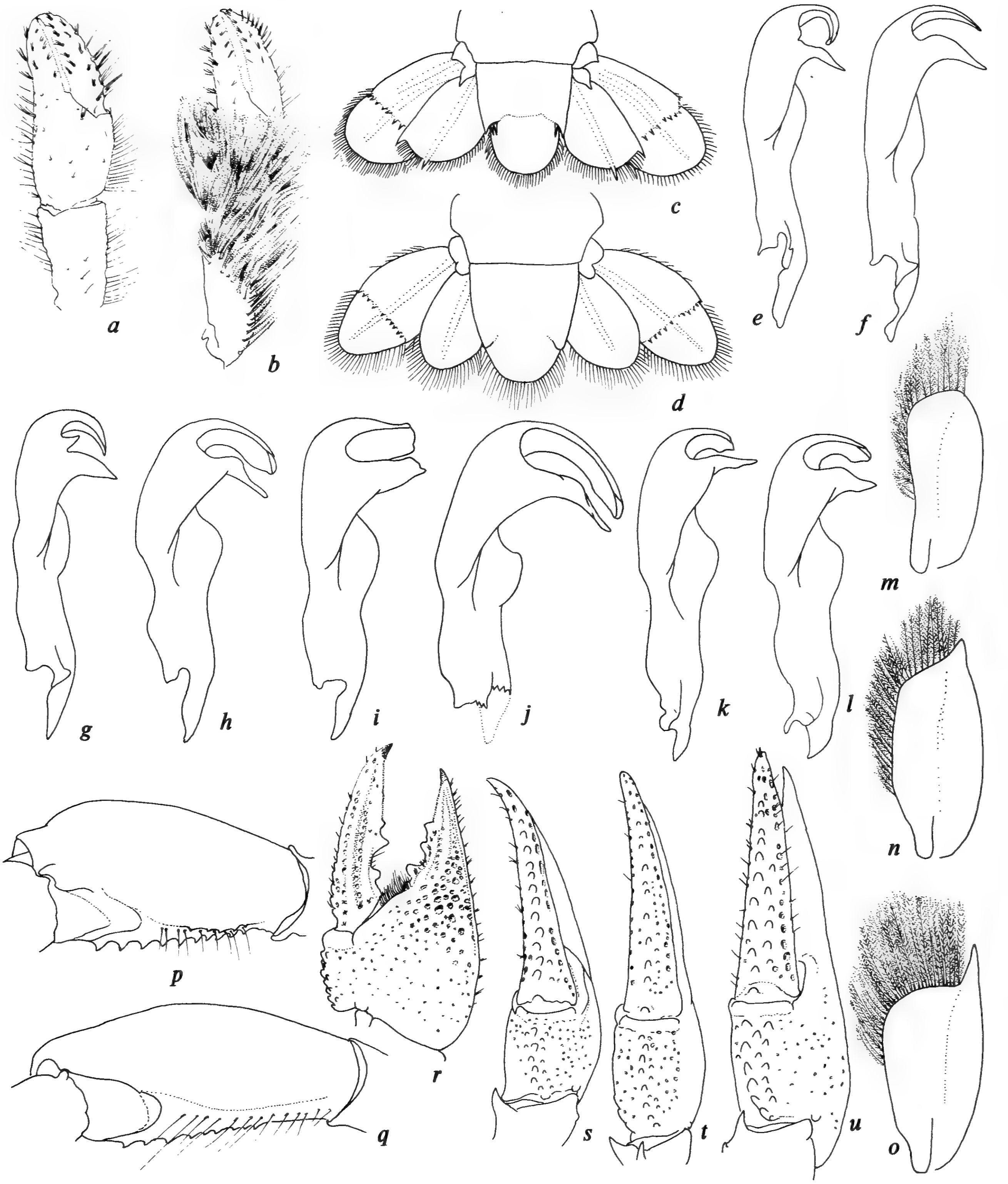

Fig. 1. Characters used in key: a, Distal podomeres of second pereiopod of *Fallicambarus* (*C.*) *byersi*; b, Same of *F.* (*C.*) *fodiens*; c, Dorsal view of telson and uropods of *F.* (*F.*) *macneesei*; d, Same from *F.* (*C.*) *jeanae*; e–l, Mesial view of first left pleopod; e, *F.* (*F.*) *dissitus*; f, *F.* (*F.*) *jeanae*; g, *F.* (*F.*) *harpi*; h, *F.* (*C.*) *byersi*; i, *F.* (*C.*) *hortoni*; *j, F.* (*C.*) *burrisi;* k, *F.* (*C.*) *danielae*; l, *F.* (*C.*) *oryktes*; m–o, Antennal scale: m, *F.* (*C.*) *burrisi*; n, *F.* (*C.*) *gordoni*; o, *F.* (*C.*) *fodiens*; p, Ventrolateral view of merus of cheliped of *F.* (*C.*) *byersi*; q, Same, *F.* (*C.*) *gilpini*; r, Dorsal view of chela of *F.* (*C.*) *caesius*; s–u, Mesial view of chela of *F.* (*C.*) *fodiens*; s, from Ohio; t, from Maryland; u, from Florida.

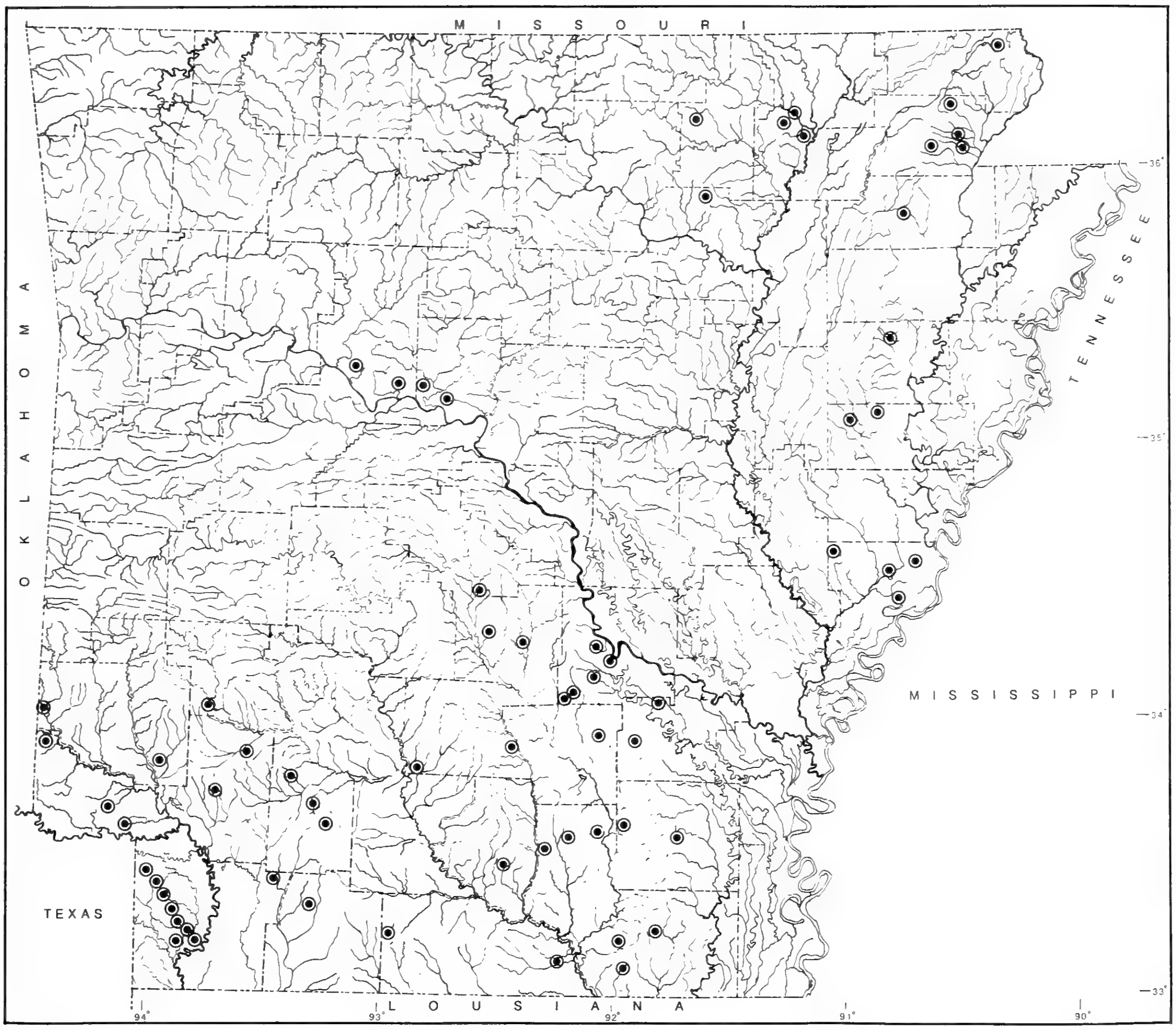

Fig. 2. Distribution of *Fallicambarus* (*F.*) *dissitus* (encircled stars), *F.* (*F.*) *jeanae* (encircled dots), *F.* (*F.*) *petilicarpus* (triangle) and *F.* (*F.*) *strawni* (dots) in Arkansas. (Some localities listed in text too close to others to be shown.)

north central Louisiana (Caldwell, Grant, and Lincoln parishes). It has been found in the following localities in Arkansas. Columbia County: (1) Southern Arkansas University Campus at Magnolia, 1 ♂ I, 23 Apr 1985, HWR. (2) 1 mi SW of Macedonia on St Rte 160, specimens not available, R. W. Bouchard and HWR. These localities lie in the Dorcheat Bayou-Red River basin.

Size.—The largest specimen that we have examined is a first form male from Lincoln Parish, Louisiana, having a cl of 32.7 (pol 29.1) mm. Corresponding lengths of the smallest first form males are 23.1 (20.2) mm.

Life history notes.—First form males have been collected in February, March, April, and May. Neither ovigerous females nor ones carrying young have been reported.

Ecological notes.—Specimens were collected in Grant Parish, Louisiana (8.2 miles, 13.2 km, south of the Winn Parish line on U.S. Highway 167), from moderately complex burrows, approximately two feet deep, in a roadside seepage area; this locality is in a rolling terrain where the soil is a sandy clay. The specimen from locality 1 was collected as it crawled across a lawn where there were chimneys 18 to 24 centimeters in height.

Fallicambarus (*Fallicambarus*) *harpi* Hobbs & Robison
Figs. 1*g*, 5

Fallicambarus (*Fallicambarus*) *harpi* Hobbs & Robison, 1985:1035–1041, fig. 1

[Types: holotype, allotype, and morphotype, USNM 217946, 217947, 217948; paratypes, MHNP, RMHL, USNM. Type locality: see page area 0.2 mi (0.32 km) east of Glenwood, Pike County, Arkansas].

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of palm of chela. Chela with lateral margin strongly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending almost complete length of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur and freely-projecting (not adnate to mesial process), caudodistally-directed cephalic process; central projection strongly arched, but not inclined laterally at base, and never crossing that of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod very strong and compressed. Mesial ramus of uropod lacking spines. Telson divided but lacking spines.

Inasmuch as no information has been added to our knowledge of this crayfish since it was described, the following data have been extracted from Hobbs & Robison (1985).

Range and specimens examined.—The two nearby localities in the Ouachita River basin cited here are the only ones known for the species. Pike County: (1) Type locality, 36 ♂ I, 13 ♂ II, 8 ♀, 1 j♂, 16 Apr 1982, K. Dillard; 2 ♂ I, 4 ♀, 21 Apr 1982, KD. (2) 0.3 mi (0.5 km) E of Glenwood on US Hwy 70, 6 ♂ I, 3 ♀, 18 Mar 1982, KD.

Color notes.—"Dorsum of cephalic region of carapace, including rostrum very dark, almost black, that of thoracic region greenish tan except for small black triangular spot in open anterior section of areola, narrow band bordering cervical groove, and another band adjacent to posterior margin of carapace; hepatic and mandibular adductor regions also black; orbital, antennal, mandibular, and branchiostegal regions greenish tan. Abdomen with broad median longitudinal, dark red stripe extending from second through fifth segment, becoming pale and disappearing before reaching caudal margin of sixth; lateral part of latter segment, telson, and uropods greenish tan with dark markings; mesial ramus of uropods with black median longitudinal rib. Dorsal surface of cheliped dark green with black suffusion becoming intense mesially so that dorsodistal border of merus, mesial part of carpus, tubercular area of palm, all of dorsum except tips of fingers and proximomesial part of fixed finger almost black; tips of fingers and lateral and ventral surfaces of entire cheliped pinkish to yellowish cream. Remaining pereiopods cream with greenish suffusion marking dorsal parts of podomeres from ischium through propodus, more intense on merus and propodus. Sternal elements and ventral surfaces of pereiopods cream to pinkish cream" (Hobbs & Robison 1985:1039).

Size.—"The largest specimen examined is a female having a carapace length of 39.6 (postorbital carapace length 35.8) mm. The smallest and largest first form males have corresponding lengths of 29.0 (25.8) mm, and 35.4 (31.5) mm, respectively" (Hobbs & Robison 1985:1039–1040).

Life history notes.—First form males were obtained in March and April. Ovigerous females or ones carrying young have not been observed.

Ecological notes.—The type locality consists of a seep "located in a pasture . . . specimens were collected in the early evening as they crawled about in the wet grassy areas. Soil consisted of a sandy clay with some organic material. Grasses and sedges were abundant. . . .”

Fallicambarus (*Fallicambarus*) *jeanae*
Hobbs
Figs. 1*d, f,* 2

Fallicambarus (*Fallicambarus*) *jeanae* Hobbs, 1973:463–469, 477, 478, 480, figs. 1, 4 [Types: holotype and allotype, USNM 144672, 144673 (♂ I, ♀); paratypes USNM. Type locality: seepage area 1.8 mi (2.9 km) E of Clark County line, Hot Spring County, Arkansas, on St Rte 84.].—Bouchard, 1978:451; 1980:451.—Bouchard & Robison, 1981:28.—Flitzpatrick, 1983: 167, 168.—Hobbs & Robison, 1985:1035, 1040.—Hobbs, 1989.

Fallicambarus (*Fallicambarus*) *spectrum* Hobbs, 1973:463, 469–478, 480, figs. 2, 4 [Types: holotype and allotype, USNM 144674, 144675 (♂ I, ♀); paratypes USNM. Type locality: 2 mi (3.2 km) E of Daisy, Pike County, Arkansas, on US Hwy 70.].—Bouchard, 1978:451; 1980:451.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:167, 168.—Hobbs & Robison, 1985:1035.

Fallicambarus jeanae.—Hobbs, 1976:550, fig. 1b, d, l.—Bouchard & Robison, 1981: 26.—Huner & Barr, 1981:50, fig 24b, d, l; 1984:45, fig. 24b, d, l.—Robison & Smith, 1982:53

Fallicambarus sp.—Hobbs, 1979:804.

Fallicambarus spectrum.—Bouchard & Robison, 1981:26.—Robison & Smith, 1982:53

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of chela. Chela with lateral margin strongly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending almost complete length of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, lacking cephalic process; central projection moderately arched, not inclined laterally at base, its distal part disposed caudoproximally, never crossing that of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod very strong and compressed. Mesial ramus of uropod lacking distolateral spine; distomedian spine, if present, situated premarginally. Telson incised laterally but lacking spines

Range and specimens examined;—This crayfish, which seems to be endemic to the upper Ouachita River basin in southwestern Arkansas, has been found in the following localities (those for which no first form males are listed should be confirmed). Clark County: (1) 1 mi (1.6 km) NE of Amity Center on St Rte 84, Sec 27NE, T5S, R23W, 2 ♂ I, 4 ♀, 1 j♂, 2 j♀, 21 Apr 1973, G. B. Hobbs, J. E. Pugh, HHH; 1 ♂ II, 2 ♀, 2 j♂, 2 j♀, 29 Apr 1976, M. Kearney, HHH; 1 ♂ II, 1 ♀, 1 j♀, 14 Apr 1979, D. D. Koym, HWR; 1 ♂ II, 3 ♀, 3 j♂, 15 Apr 1982, HWR, DDK. (2) roadside ditch 7.4 mi (11.8 km) E of Amity Center on St Rte 84, 1 ♂ I, 1 ♀, 3 j♂, 30 Apr 1976, MK, HHH. (3) Richland Cemetery, 3 mi (4.8 km) NW of Gum Springs, 1 j♂, 1 j♀, 24 Feb 1980, W. Laird. (4) Rest Haven Cemetery 4 mi (6.4 km) W of Arkadelphia on St Rte 8, 1 ♀, 1 j♂, 1 j♀, 24 Sep 1977, E. Laird; 1 j♂, 27 Dec 1979, EL; 3 ♀, 6 May 1980, EL; 2 ♀, 1 j♂, 1 j♀, 12 Feb 1981; 2 ♂ II, 4 ♀, 6 j♂, 5 j♀, 9 Mar 1981, EL, HWR; 1 ♀, 19 Mar 1981, EL. Hempstead County: (5) Blevins, Sec 24, T9S, R24W, 3 ♀, 1 j♂, 29 Apr 1983, P. Lee. (6) Blevins, Sec 6, T10S, R24W, 1 j♂, 1 j♀, 10 May 1983, B. Hill. (7) Blevins, Sec 35, T9S, R25W, 1 ♀, 16 May 1983, T. Chambers. Hot Spring County: (8) roadside ditch 1.8

mi (2.9 km) E of Clark Co line on St Rte 84 (Type locality), 5 ♂ I, 2 ♀, 3 j♂, 2 j♀, 21 Apr 1973, GBH, JEP, HHH. (9) roadside ditch 3.7 mi (5.9 km) E of jct of St Rtes 7 and 84 on latter, 2 ♂ I, 1 j♀, 30 Apr 1976, MK, HHH. (10) roadside ditch 5.2 mi (8.3 km) E of Clark Co line on St Rte 84, 1 j♀, 30 Apr 1976, MK, HHH. (11) roadside ditch 4.5 mi (7.2 km) W of Marcus, 3 ♂ I, 1 ♂ II, 2 ♀, 2 j♂, 5 j♀, 14 Apr 1979, HWR et al. (12) 2.1 mi (3.3 km) E of Point Cedar, 2 ♀, 1 j♂, 1 j♀, 13 Mar 1981, HWR; 1 ♂ I, 2 ♀, 3 j♂, 15 Apr 1982, HWR, DDK. Pike County: (13) roadside ditch 2 mi (3.2 km) E of Daisy on US Hwy 70, 1 ♂ I, 1 ♀, 21 Apr 1973, GBH, JEP, HHH. (14) roadside ditch 2.8 mi (4.5 km) W of Amity Center on St Rte 84, 2 ♂ II, 3 ♀, 2 j♂, 14 Apr 1979, HWR et al. (15) roadside ditch 8.2 mi (13.1 km) W of Amity Center on St Rte 84, 1 j♀, 14 Apr 1979, HWR et al.

Remarks.—With the acquisition of considerably more material than was available to him when *Fallicambarus* (*F.*) *spectrum* was described, Hobbs (1989) concluded that except by the color pattern this crayfish cannot be distinguished from *F.* (*F.*) *jeanae.* The pattern of the former, which is described below, has been observed only in specimens from the type locality. He therefore treated *spectrum* as a color morph of *F.* (*F.*) *jeanae.*

Color notes.—*Fallicambarus* (*F.*) *jeanae* exhibits two distinctive color morphs; that occurring in specimens from the type locality was described by Hobbs (1973:468) as follows: "Dominant color of carapace pale mauve; rostral margins, postorbital ridges, and paired subtriangular areas caudal to postorbital ridges dark brown; latter joining along cervical groove and in caudal gastric area where almost black; caudal margin of carapace dark brown. First abdominal tergum dark brown, remaining ones pale yellowish tan with paired dorsolateral cream splotches and each edged caudally with vermilion. Telson and uropods cream with pale tan suffusion basally. Antennule and antenna with dark yellowish-brown peduncles; flagella with each article yellowish tan basally and dark brown distally; lateral margin of antennal scale almost black. Cheliped mostly yellowish tan dorsally with dark bluish-brown tubercles and bluish-brown suffusion on dorsal margin of merus, dorsomesial surface of carpus, and dorsomesial part of dactyl. Ventral surface of cheliped yellowish cream. Remaining pereiopods with coloration similar to that of cheliped but lacking dark brown tubercles."

The color of the morph that was described under the name of *Fallicambarus* (*F.*) *spectrum* (Hobbs, 1973:472–473) was recorded as follows: "Dominant color of carapace pale mauve gray; rostral margins and postorbital ridges almost black; paired subtriangular reddish-brown markings extending caudally from caudal extremity of postorbital ridges, their basal portions coalescing in median posterior gastric region, slightly overlapping cervical groove, and filling cephalic triangular vestige of areola. Hepatic region with pale reddish-tan suffusion; caudal margin of carapace edged with black. [Dorsolateral parts of branchiostegites provided with conspicuous dark bluish purple (some almost black) spots.] First abdominal tergum reddish brown with succeeding terga progressively fading to uniformly reddish-tan telson and uropods; tergum also fading laterally, and pleuron concolorous with telson. Peduncle of antennule and antenna dark mauve gray, flagella with each article pale tan proximally, becoming dark gray distally; antennal scale with lateral thickened portion almost black. Chelipeds grayish blue dorsally with dark blue tubercles; ventral surface cream; remaining pereiopods similar to cheliped but lacking dark blue tubercles."

Size.—The largest specimen examined by us is a female from Clark County having a cl of 40.6 (pol, 35.5) mm. The smallest and largest first form males have corresponding lengths of 30.0 (26.4) mm and 35.7 (31.7) mm, respectively.

Life history notes.—All of the first form males that we have examined were collected in April. Neither ovigerous females nor ones carrying young have been observed. A first form male and female were found occupying a single burrow at locality 1 on 21 Apr 1973.

Ecological notes.—The largest colony of this crayfish that we have observed was in the type locality. Persistent rains for at least several days while one of us (HHH) was in the area had brought the water table throughout the seep to the surface, and the mounds marking the entrances to the crayfish burrows were considerably eroded. They did not appear to have been neatly constructed, and the pellets of which subsequently observed turrets were constructed by *F.* (*F.*) *jeanae* seemed to have been rather haphazardly affixed to the rim, many having rolled down the side of the crude, vaguely cone like structures. The soil was primarily a sandy clay with gravel and pockets of organic material. The burrows were rather shallow (most of the horizontal passages coursed at depths of 10 to 30 cm; the one or two deeper passages no doubt penetrated the soil for 70 cm to one meter), highly branching, and had two or three openings to the surface. In the immediate vicinity, grasses and sedges were growing in the waterlogged soil, and nearby were trees belonging to the genera *Acer, Juniperus,* and *Pinus.* In April of 1973, the soil was so lacking in firmness that no tool was needed to aid the hand in searching for the crayfish in their burrows. In localities 1 and 13, where the "*spectrum* color morph" was found, the soil was better drained (a small, clear brook flowed through locality 1), the burrows were deeper (but extended no more than a meter beneath the surface), and the horizontal galleries were restricted to a smaller surface area.

Fallicambarus (*Fallicambarus*) *petilicarpus,* new species
Figs. 2, 3, 4a

Diagnosis.—Eyes small but pigmented and with faceted cornea. Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus greater than width of palm of chela. Chela with lateral margin weakly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl lacking pronounced excision in basal half, mesial margin with row of tubercles along at least proximal third. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, and free, caudally projecting cephalic process; central projection strongly arched, inclined laterally at base but projecting mesially and crossing that of corresponding pleopod distally. Hooks on ischia of third and fourth pereiopods. Boss on coxa of fourth pereiopod moderately strong and compressed. Mesial ramus of uropod with distolateral spine, distomedian spine, if present, situated premarginally. Telson divided and with spine/s on anterolateral flank of suture.

Holotypic male, form I.—Body suboval, weakly compressed laterally (Figs. 3*a, l,* 4*a*). Abdomen distinctly narrower than thorax (9.6 and 14.5 mm). Greatest width of carapace near midlength of areola where subequal to height (14.5 and 14.2 mm). Areola linear over most of length and comprising 37.4 percent of entire length of carapace (42.9 percent of postorbital carapace length). Rostrum with convergent, slender margins contracting anteriorly, setting off base of indistinctly delimited acumen, apex of which corneous, upturned, and slightly overreaching midlength of penultimate podomere of antennular peduncle. Dorsal surface of rostrum strongly concave, with submarginal rows of setiferous punctations and scattered ones between. Subrostral ridges rather weak but evident in dorsal aspect to base of acumen. Postorbital ridges also weak but somewhat swollen posteriorly. Branchiostegal and cervical spines absent. Suborbital angle absent. Carapace punctate dorsally and very weakly and sparsely tuberculate laterally;

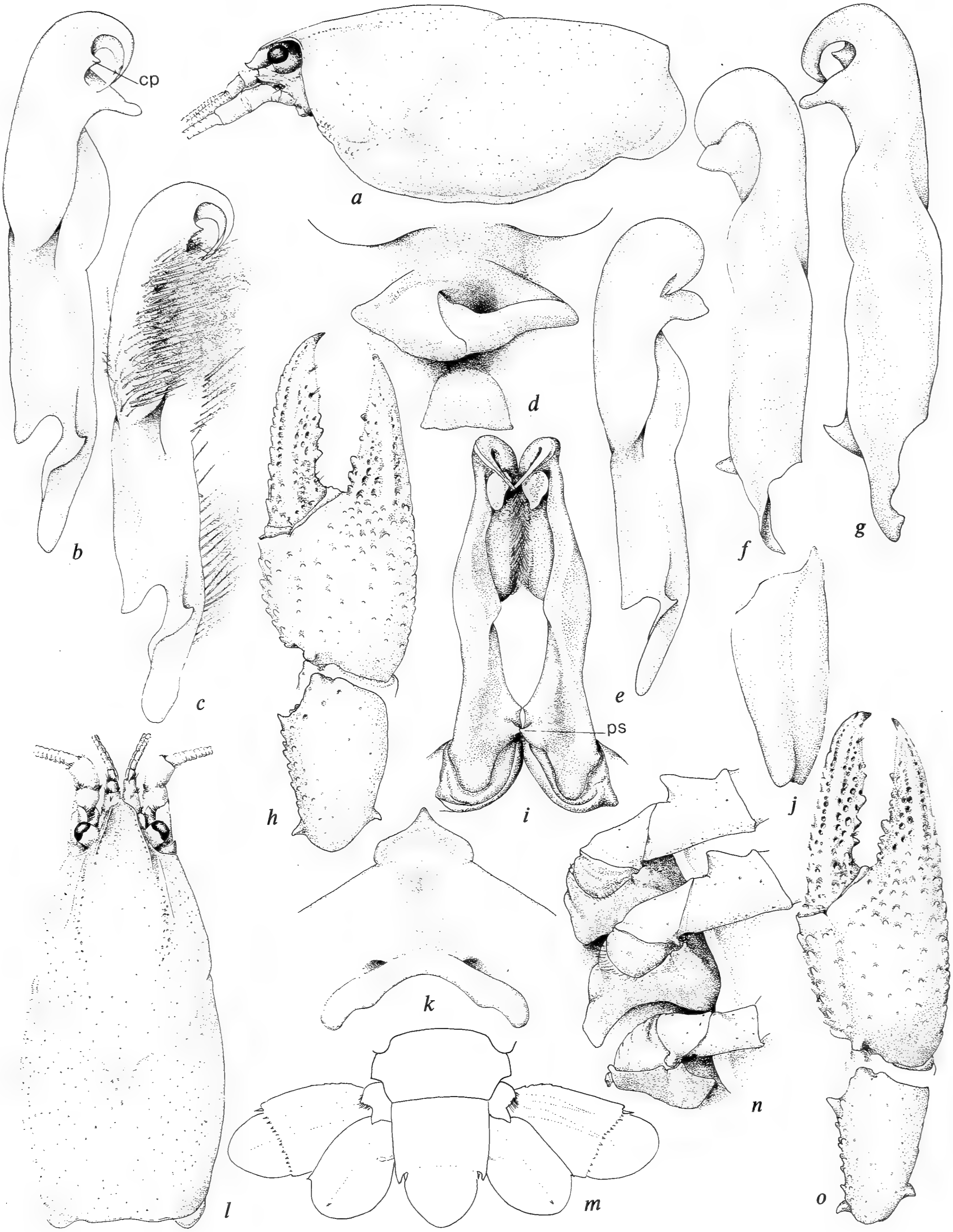

Fig. 3. *Fallicambarus* (*F.*) *petilicarpus* holotype except d, h, j from allotype, and e, f from morphotype): a, Lateral view of carapace; b, c, e, Mesial view of first pleopod, cp cephalic process; d, Annulus ventralis and associated sclerites; f, g, Lateral view of first pleopod; h, o, Distal podomeres of cheliped; i, Caudal view of first pleopods; j, Antennal scale; k, Epistome; l, Dorsal view of carapace; m, Dorsal view of caudal part of abdomen; n, Basal podomeres of third, fourth, and fifth pereiopods. (cp, cephalic process; ps, proximomesial spur.)

extreme anteroventral branchiostegal region inflated, with irregular group of tubercles, seven or eight forming row on ventral flank of cervical groove; fewer tubercles present on dorsal flank of groove.

Abdomen (Fig. 4*a*) little shorter than carapace (28.0 and 30.5 mm); pleura moderately deep and broadly rounded ventrally, only sixth with angular caudoventral margin; pleuron of first abdominal segment clearly overlapped by that of second. Telson (Fig. 3*m*) distinctly divided, and caudolateral angles of anterior section with two pairs of spines, more mesial pair movable. Proximal podomere of uropod with both lobes bearing distal spine, spine on more mesial lobe much stronger than that on lateral lobe; mesial ramus with well developed distolateral spine and smaller premarginal distomedian spine.

Cephalomedian lobe of epistome (Fig. 3*k*) broadly subtriangular with well defined cephalomedian prominence extending cephalodorsally; cephalolateral margins rather smooth; main body of epistome with cephalomedian area depressed but lacking distinct fovea. Ventral surface of proximal podomere of antennule with median spine slightly distal to midlength. Antennal peduncle without spines except on lateral surface of basis at proximal base of antennal scale, flagellum reaching second abdominal tergum. Both antennal scales of holotype with distal extremities missing, but distinctly reduced: blade little broader than thickened lateral portion and apex probably reaching only slightly beyond midlength of penultimate podomere of antennule (see Fig. 3*j, l*). Mandible essentially like that of *Fallicambarus* (*F.*) *devastator* Hobbs & Whiteman (1987: fig. 1i). Ventral surface of ischium of third maxilliped with lateral row of short, plumose setae, and mesial half studded with clusters of long, stiff setae.

Right chela (Fig. 3*o*) approximately 2.4 times as long as broad, not strongly depressed; width of palm slightly more than 1.2 times length of mesial margin, latter bearing row of 7 tubercles subtended dorsolaterally by row of six (left with 6 and 7, respectively); dorsal surface of palm and basal part of fingers studded with squamous tubercles; those along lateral margin forming subserrate row extending from near proximal extremity to about midlength of fixed finger; ventral surfaces of palm, basal third of fixed finger, and mesial part of proximal fourth of dactyl tuberculate; more distoventral part of fingers with punctations, in part, flanking weak median ridges; prominent spiniform tubercle present on oblique distoventral ridge of palm; ventrolateral surface lacking curved row of long setae. Opposable margin of fixed finger with row of 7 tubercles (fourth from base largest) in proximal three-fifths and another (corresponding to usually more ventrally-placed tubercle on the chelae of most cambarids) at base of distal third; minute denticles present between distal 4 tubercles, and, except at base of distalmost tubercle, continuing to corneous tip of finger. Opposable margin of dactyl with row of 5 tubercles (third from base largest; this tubercle marking end of sharp proximal excavation in dactyl of other members of *Fallicambarus*) in proximal three-fourths; mesial margin of dactyl with tubercles forming subserrate row. Dorsal surface of both fingers with well defined median longitudinal ridge.

Carpus of cheliped conspicuously slender and long, almost 1.6 times as long as broad, and longer than either width or mesial margin of palm of chela. Dorsal surface sparsely punctate and bearing poorly delimited and very shallow, oblique, longitudinal furrow; mesial surface with only one prominent subspiniform tubercle, cluster proximoventral to it consisting of much smaller ones; except for ventrodistal extremity bearing usual 2 moderately large tubercles, ventral and lateral surfaces punctate. Merus with single, dorsal, slightly curved row of tubercles, increasing in size distally; lateral surface punctate, and mesial one with polished and granular areas; ventral surface with both mesial and lateral rows of 15 tubercles joined by oblique row of 3. Mesioventral margin of basioischial podomere with only 2 tubercles corresponding to row in other crayfishes; compound podomere otherwise with scattered punctations. Chela of second pereiopod with marginal row of setae on palm, and carpus with dorsal row of long setae; mesial surface of carpus and propodus lacking tufts of plumose setae.

Ischia of third and fourth pereiopods (Fig. 3*n*) with simple hooks, neither of which overreaching basioischial articulation and neither opposed by tubercle on corresponding basis. Coxa of fourth pereiopod with prominent, compressed caudomesial boss disposed somewhat in longitudinal axis of body; mesial and lateral surfaces of boss with setiferous punctations. Coxa of fifth pereiopod with small tuberculiform boss extending ventrally from caudomesial angle of podomere; ventral membrane setiferous.

First pleopods (Fig. 3*b, c, g, i*) reaching coxae of third pereiopods, carried deeply in sternum, and largely concealed by setae extending from ventral margin of sternum and from coxae of third and fourth pereiopods. Proximomesial spur well developed. Shaft of appendage only slightly inclined caudally; plumose setae arising from mesial surface of shaft forming feathery plume hiding all or part of each of three terminal elements: mesial process, most proximal of three, non-corneous, somewhat tapering but with rounded apical region, disposed at slightly more than right angle to shaft of appendage; cephalic process smallest, corneous, subtriangular, situated between cephalic process and central projection, and directed caudally; and central projection most conspicuous of three, consisting of long, tapering, bladelike structure reflexed through arc of at least 150 degrees.

Allotypic female.—Differing from holotype other than in secondary sexual characteristics as follows: acumen even less distinctly delimited basally; subrostral ridges evident in dorsal aspect for no more than one-fifth distance from caudal margin of orbit to base of acumen; rudiment of branchiostegal spine present; about same number of tubercles (7 or 8) on both dorsal and ventral flanks of anteroventral segment of cervical groove; spine on lateral lobe of proximal podomere of uropod rudimentary; spine on basis of antenna tuberculiform; flagellum of antenna extending caudally over no more than three-fourths length of areola; chela (Fig. 3*h*) proportionally shorter and broader; mesial row of tubercles on palm of chela subtended dorsally by row of only 5 tubercles; opposable margin of fixed finger with row of 5 tubercles, third from base largest; opposable margin of dactyl with row of 4 tubercles, second from base largest; ventral surface of merus of cheliped with mesial and lateral rows of 14 tubercles; mesioventral margin of basioischial podomere with 3 tubercles (left chela regenerated).

Annulus ventralis (Fig. 3*d*) firmly fused to sternum cephalically, approximately twice as broad as long, and strongly asymmetrical. Cephalic and cephalomedian areas depressed, latter distinctly excavate; dextral side of excavation elevated in massive prominence along mesial margin of which C-shaped sinus marking junction of prominent transverse ridge and prominence; no clearly defined sulcus evident, and fossa hidden. Postannular sclerite about 1.7 times as broad as long and less than half as wide as annulus; lateral margins weakly converging toward broadly rounded anterior extremity; caudal margin irregularly transverse. First pleopods present but not reaching anterior to postannular sclerite.

Morphotypic male, form II.—Differing from holotype as follows: Apex of rostrum reaching base of ultimate podomere of antennule; right branchiostegal spine represented by very small tubercle; proximal podomere of uropod lacking spine on both lobes; antennal peduncle lacking spine on basis, flagellum reaching first abdominal tergum; (as in holotype, distolateral part of both antennal scales broken); chela approximately 2.2 times as long as broad; left chela with only 6 tubercles in mesialmost row on palm; merus of left cheliped with lateral row of only 12 tubercles; mesioventral margin of basioischial podomere with row of 3 or

4 tubercles; hooks on ischia of third and fourth pereiopods and boss on coxa of latter all clearly defined but weaker than those in holotype.

First pleopods (Fig. 3*e, f*) reaching coxae of third pereiopods, symmetrical, and with well defined proximomesial spur; markedly similar in form to pleopod of first form male, but lacking cephalic process, and base of central projection not nearly so distinctly delimited from mesial process.

Color notes.—Basic coloration olive-brown to tan. Carapace dark olive-brown; rostrum and posterior gastric area very dark; lateral areas slightly paler. First abdominal tergum dark olive-brown, second through fifth paler olive-tan and with narrow pinkish tan arc on posteromedian margins; sixth tergum, telson, and uropods dark olive. Antennules and antennae with peduncles olive on brown; flagella reddish brown. Chelipeds with basal three podomeres and proximal part of merus pinkish cream, latter suffused dorsally and laterally with olive, becoming dark olive distally; dorsal tubercles on merus green with white tips. Dorsal and lateral surfaces of carpus bright olive to forest green on brown, tubercles green and largest ones tipped with cream. Chela olive-brown dorsally; distal ridge on palm suffused with green, and green on dorsal flank of opposable borders of both fingers; palm and fixed finger fading ventrolaterally to pinkish orange, ventral surface of all podomeres of cheliped pinkish to lavender cream. Remaining pereiopods with olive suffusing distal part of merus, carpus, and, except that of second pereiopod, proximal part of merus, otherwise pale pinkish cream.

Size.—The largest specimen examined is a female having a cl of 31.8 (pol 27.6) mm. The smaller of the two known first form males, the holotype, has corresponding lengths of 30.5 and 26.6 mm, respectively. Neither ovigerous females nor ones carrying young are available for determining measurements.

Type locality.—Roadside seepage 0.2 mile east of the Columbia County line on State Route 57, Union County, Arkansas (T16S, R18W, Sec 21). A field of young planted trees (*Pinus*) was adjacent to the seep and ditch which supported a moderate growth of sedges and grasses. Specimens were collected from relatively shallow, but complex burrows which, constructed in a sandy loam and topped by chimneys from 8 to 10 cm high, descended to depths of approximately 0.5 m. Some of them penetrated tangled, dense root mats of grasses growing in and on the banks of the ditch. No other crayfish was found in the immediate area.

Disposition of types.—The holotype, allotype, and morphotype (USNM 219507, 219508, and 219509, respectively) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of 1 ♂ I, 1 ♂ II, 3♀, and 9 juveniles.

Range and specimens examined.—All of the specimens available were collected at the type locality by the second author on 30 Apr 1982 (1 ♂ I, 1 ♂ II, 2 ♀, and 3 juv) and 28 Mar 1988 (1 ♂ I, 2 ♂ II, 2 ♀, 6 juv).

Variations.—Among the adult specimens, the areola constitutes from 35.2 to 38.5 percent of the total length of the carapace, and from 39.8 to 43.6 percent of the postorbital carapace length. In one small male with a carapace length of 21.5 mm, the corresponding ratios are 34.0 and 39.0 percent, respectively. Most of the variations noted fall within the range of those noted in the descriptions of the primary types. The greatest range of differences, barring regenerated appendages, occurs in the numbers of tubercles on the chelipeds: the opposable margin of the fixed finger may have from 4 to 8 tubercles and that of the dactyl 4 to 7; the ventromesial row on the merus ranges from 14 to 16 and the mesiolateral, from 12 to 15. In the female the annulus ventralis occurs in mirrored images of that in the allotype, and the cephalic margin may or may not be firmly fused to the sternum immediately anterior to it. All of the females have a linear series of 3 to 5 long setae closely associated with the distal part of the ven-

Table 1.—Measurements (mm) of *Fallicambarus* (*F.*) *petilicarpus*.

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	30.5	29.5	29.5
Postorbital length	26.6	25.8	26.6
Width	14.5	13.9	13.0
Length	14.2	13.3	12.6
Areola:			
Width	0	0	0
Length	11.4	11.1	10.2
Rostrum:			
Width	4.4	4.2	4.6
Length	5.1	4.5	4.8
Right chela:			
Length, palm mesial margin	9.3	4.6	7.3
Palm width	10.9	8.0	8.9
Length, lateral margin	24.5	16.1	19.4
Dactyl length	14.6	10.5	11.2
Abdomen:			
Width	9.6	10.1	9.0
Length	28.0	27.3	26.0

trolateral row of tubercles on the merus; such seem not to be present in the available males. (See Table. 1 for other morphometric differences.)

Life history notes.—The only collections of this crayfish available are two lots collected at the type locality in March and April. A first form male was obtained in both samples. Ovigerous females and ones carrying young have not been observed.

Ecological notes.—See "Type locality."

Relationships.—*Fallicambarus* (*F.*) *petilicarpus* is more closely allied to *F.* (*F.*) *dissitus* than to any other member of the genus. The unusual first pleopods of the males of the two species with caudomesially disposed, crossing (at least sometimes) central projections, are so nearly alike that only after a detailed re-examination of specimens of the former was the distinctive feature, the presence of a small, but well-defined cephalic process, observed. Subsequent comparisons of the two revealed, among the many similarities, two other readily observed features that set *F.* (*F.*) *petilicarpus* apart: the very long slender carpus of the first cheliped and the unique absence in *Fallicambarus* of a distinct concavity on the opposable margin at the base of the dactyl of the chela. The absence of this concavity, a feature the presence of which has served in keys until now to distinguish members of the genus *Fallicambarus* from *Cambarus*, necessitated the slight modifications in the generic diagnosis included herein.

Etymology.—The name describes the slender carpus of the cheliped: *Petilus* (L. = slender) + *carpus* (L. = wrist).

Fallicambarus (*Fallicambarus*) *strawni* (Reimer)

Figs. 2, 10*y*

Cambarus strawni Reimer, 1966:9, 11–14, figs. 9–18 [Types: holotype, allotype, and morphotype, USNM 116675, 116676, 116677 (♂ I, ♀, ♂ II); paratypes, R. D. Reimer. Type locality: small marshy area in the Saline River basin, 2.7 mi (4.3 km) north of Dierks, Howard Co., Arkansas.].—Hobbs, 1967:12; 1968:K16, fig. 32; 1969a:111.—Black, 1967:173, 178.—Bouchard, 1972:61.—Hobbs III et al., 1976:24.

Fallicambarus strawni.—Hobbs, 1969a:103, 111, 124, 151, 173, figs. 2f, 13j, 20i; 1972: 99, 147, fig. 81b; 1974b:24, 100, fig. 81; 1976:551, fig. 1b, e.—Bouchard & Robison, 1981:26.—Robison & Smith, 1982: 53.

Fallicambarus (Fallicambarus) strawni.—Hobbs, 1973:461–479, figs. 3c, h, 4.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:168.—Hobbs & Robison, 1985:1035.

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of palm of chela. Chela with lateral margin strongly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending almost complete length of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, and cephalic process adnate to mesial process, if free distally, then directed caudally, parallel to mesial process; central projection comparatively weakly arched, not inclined laterally at base, and disposed caudally, never crossing that of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod very strong and compressed. Mesial ramus of uropod lacking distolateral spine, distomedian spine, if present, situated premarginally. Telson entire, lacking spines.

Range and specimens examined.—This crayfish seems to be endemic to southwestern Arkansas (although there is every reason to believe that it will be found in eastern Oklahoma) where it has been collected only in the Little and Saline watersheds in the Red River basin and in the Little Missouri watershed in the Ouachita River basin. We have examined all of the following material except that collected in locality 6. Howard County: (1) Type locality, 1 ♂ I, 1 ♂ II, 1 ♀, 22 Jun 1963, R. D. Reimer; 2 ♂ I, 1 ♂ II, 1 ♀, 1 j♂, 1 j♀, 21 Apr 1973, GBH, JEP, & HHH; 1 ♀, date ?, R. W. Bouchard. (2) roadside ditch 5.1 mi (8.2 km) W of Athens on St Rte 84, 1 ♂ I, 1 ♀, 29 Apr 1976, MK & HHH. (3) seep 1.8 mi (2.9 km) E of Polk Co line on St Rte 4, 3 ♀, 3 ♂ II (one ♂ later molted to form I), 29 Apr 1976, MK & HHH. (4) roadside ditch 1.8 mi (2.9 km) E of Sevier Co line on US Hwy 70, 3 j♂, 6 j♀, 10 Apr 1982, HWR. (5) Nashville, 1 ♂ II, 10 Apr 1986, L. Morris. (6) Reimer (1966: 4) cited this crayfish from 4 mi W of Umpire on St Rte 4. Pike County: (7) roadside ditch 1.3 mi (2.1 km) E of Little Missouri River on St Rte 84, 1 ♀, 1 j♂, 29 Apr 1976, MK, HHH. (8) roadside ditch 0.9 mi (1.4 km) NE of Howard Co line on US Hwy 70, 1 ♂ I, 1 ♀, 21 Apr 1973, GBH, JEP, HHH. Sevier County: (9) seep and ditch 0.1 mi (16 km) NE of jct of US Hwys 71-59 and 70 on latter, 4 ♂ I, 4 ♂ II, 13 ♀, 2 j♂, 5 j♀, 20 Apr 1973, GBH, JEP, HHH. (10) seep 8.3 mi (13.3 km) E of jct of US Hwys 59-71 and 70 on latter, 1 j♀, 28 Apr 1976, MK, HHH. (11) seep 0.2 mi (0.32 km) E of jct of US hwys 71 and 59 on latter, 1 j♂, 1 ♀, 26 Apr 1976, RWB. (12) 5.8 mi (9.3 km) E of jct on St Rtes 41 and 24 on latter, 1 j♂, 9 Apr 1982, HWR. (13) seep 5.0 mi (8.0 km) NE of jct of US Hwys 59-71 and 70, 1 ♂ I, 20 Apr 1973, GBH, JEP, HHH.

Color notes.—(Based primarily on first form male from locality 8.) Dominant color of carapace pinkish cream to purplish tan overlain by various shades of gray and vermilion. Most of dorsum of cephalic region pinkish tan fading laterally to buff, often with lavender suffusion; rostrum and postorbital ridges very dark gray margined in almost black; caudal gastric area and cervical groove pale to dark gray; cephalic triangle of areola dark gray to almost black, and linear part and caudal triangle of areola vermilion; paired pale gray longitudinal stripes flanking linear areola; remainder of branchiostegites, excluding dark bluish gray caudal margin, very pale cream tan. Tergum of first abdominal segment and cephalic part of that of second dark bluish red, otherwise yellowish tan with vermilion splotches dorsally, fading caudally, and all pleura lighter tan ventrally. Telson largely translucent but with vermilion to brick red splotches cephalically, laterally, and along caudal margin; uropod similarly translucent, but peduncle reddish tan, lateral ramus with reddish splotches lateral to median rib and over entire distal section, and mesial ramus with red pigment largely restricted to median rib and distal third. Chelipeds basically tan but with dense reticulations of slate blue on dorsum of distal half of merus, that of carpus, and most of that of chela; lateral surface of palm pinkish cream. Exposed parts of peduncles of antennule and antenna mostly gray, and flagella with each article buff proximally, becoming dark gray distally. Lateral margin of antennal scale very dark gray. Remaining pereiopods similar to cheliped, although with more red and less blue pigment on fifth. Ventral surface of body and pereiopods cream, latter with blue pigment toward distal ends of merus and carpus.

In first form male from locality 2 (Howard County), dorsal cephalic region darker orange tan, and with dark brownish-gray area extending across posteromedian gastric region abutting cervical groove; thoracic region more apricot-colored dorsally, fading to cream tan ventrally; anterior triangle of areola almost black, branchiocardiac suture vermilion to scarlet, and posterior triangular area dark reddish brown. Abdomen much darker than carapace, terga of first two segments almost black anteriorly fading rapidly to brick red caudally; succeeding segments with paired subrectangular reddish black splotches (gradually narrowing on posterior segments) dorsolaterally, flanking median glossy brick red longitudinal stripe, red spreading laterally on posterior part of each segment and spilling ventrally onto dorsal part of pleura, which mostly pale pinkish cream with posterior maroon spot. Telson, uropods, and chelae as described above.

Size.—The largest specimen available is a female from Sevier County (locality 9, above) having a cl of 37.2 (pol 32.4) mm. The smallest and largest first form males have corresponding lengths of 24.8 (22.2) mm and 31.9 (28.5) mm, respectively.

Life history notes.—First form males have been collected in April and June. Neither ovigerous females nor ones carrying young have been observed.

Ecological notes.—This crayfish, like *F.* (*F.*) *jeanae,* constructs highly branching (complex) burrows in sandy clay soil. The largest colony visited by us was found at locality 9. There the roadbed is somewhat elevated above the adjoining wooded area (chiefly *Pinus*), and on the northern shoulder of the elevated area, there is a seep in which scores of turrets mark the burrows of this crayfish. When one of us (HHH) first visited this locality in April 1973, the sandy clay soil was water-logged, and one could easily open and follow the complex system of galleries with one's bare hands. On a visit three years later, following a period without rain, there were few turrets in the hard, dry ground, and, even with the aid of a shovel and considerable effort, only one juvenile was found!

Subgenus *Creaserinus* Hobbs (1973)

First pleopod never with proximomesial spur or cephalic process. Cheliped with sufflamen; chela with tubercles on mesial surface of palm but sparse or lacking dorsolaterally and laterally, lateral margin costate. Second pereiopod of male with mesial face of chela and carpus often bearing dense mats of plumose setae (lacking in *F.* (*C.*) *burrisi, F.* (*C.*) *byersi, F.* (*C.*) *caesius, F.* (*C.*) *gilpini,* and *F.* (*C.*) *gordoni*). Type species: *Astacus fodiens* Cottle, 1863:217. Gender: masculine.

Fallicambarus (*Creaserinus*) *caesius* Hobbs
Figs. 1*r,* 5

Fallicambarus (*Creaserinus*) *caesius* Hobbs, 1975:24–28, 33, fig. 7 [Types: holotype, allotype, and morphotype, USNM 144921, 133922, 133923 (♂ I, ♀, ♂ II); paratypes, USNM. Type locality: Roadside ditch at Hot Spring-Saline county line, Arkansas, on St Rte 67.]; 1981:269.—Bouchard, 1978:451; 1980:451.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:168; 1987:439.

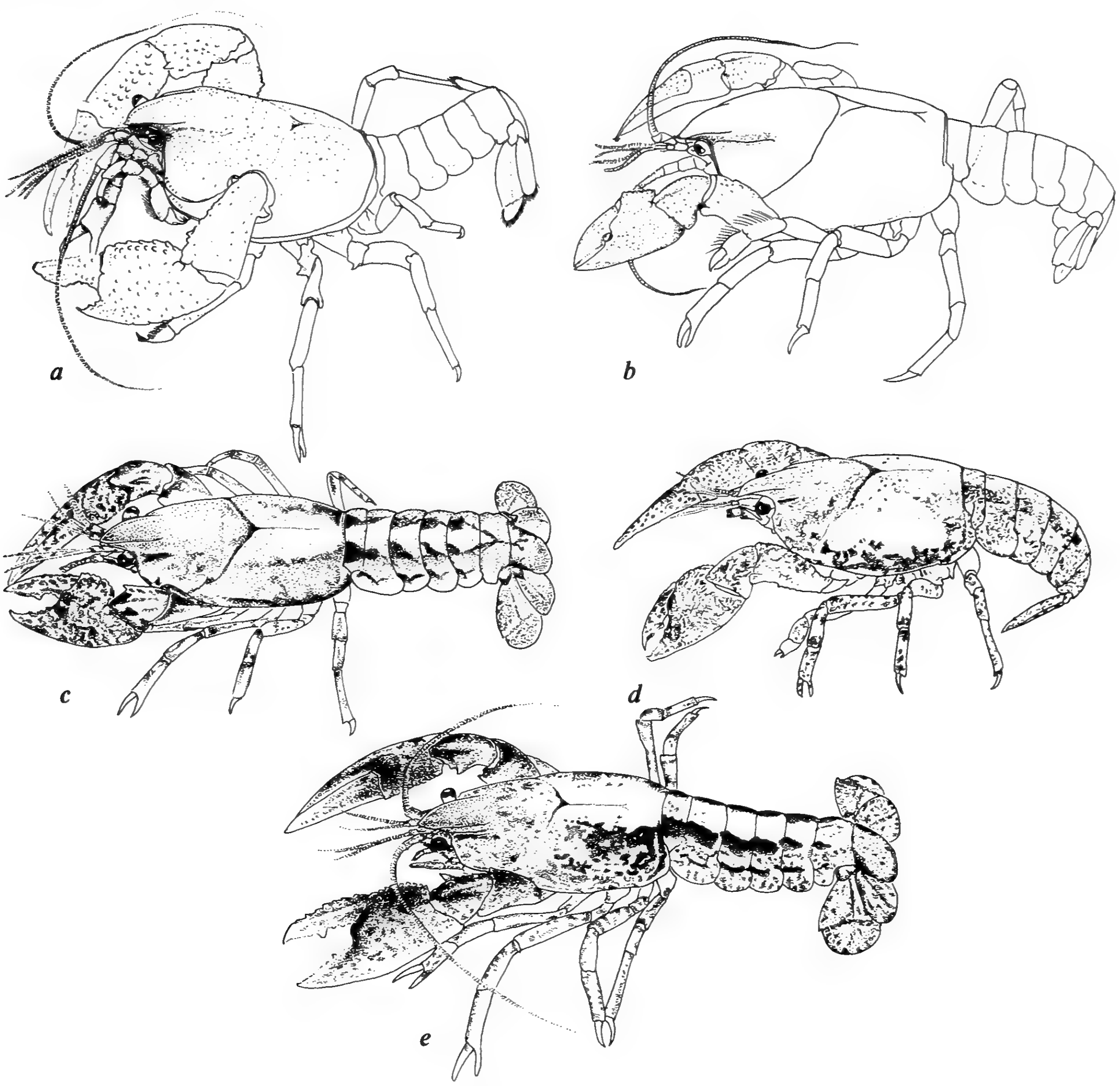

Fig. 4. Dorsolateral views of *Fallicambarus*: a, *F.* (*C.*) *petilicarpus*; b, *F.* (*F.*) *gilpini*; c–e, *F.* (*C.*) *fodiens* from: c, Independence County, Arkansas; d, Santa Rosa County, Florida; e, Orangeburg County, South Carolina.

Fallicambarus caesius.—Hobbs, 1975:28.—Bouchard & Robison, 1981:26.

Diagnosis.—Ventral surface of merus of cheliped with mesial row of tubercles, lateral one never represented by more than 2. Lateral margin of chela strongly costate, never serrate, dorsal surface without scattered tubercles in lateral half, ventrolateral surface with arched row of prominent punctations bearing long setae; opposable margin of dactyl with longitudinal row of tubercles extending along at least proximal third of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod without proximomesial spur, and lacking cephalic process; central projection weakly arched, its base not inclined laterally, its distal part directed caudoproximally, bearing well defined subapical notch, and never crossing central projection of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod somewhat rounded, neither strongly compressed nor conspicuously protruding ventrally. Mesial ramus of uropod with or without distolateral spine; distomedian spine premarginal. Telson incompletely divided and with or without spine on anterolateral flank of suture.

Range and specimens examined.—Insofar as is known, this crayfish is endemic to Arkansas where it is confined to the Oua-

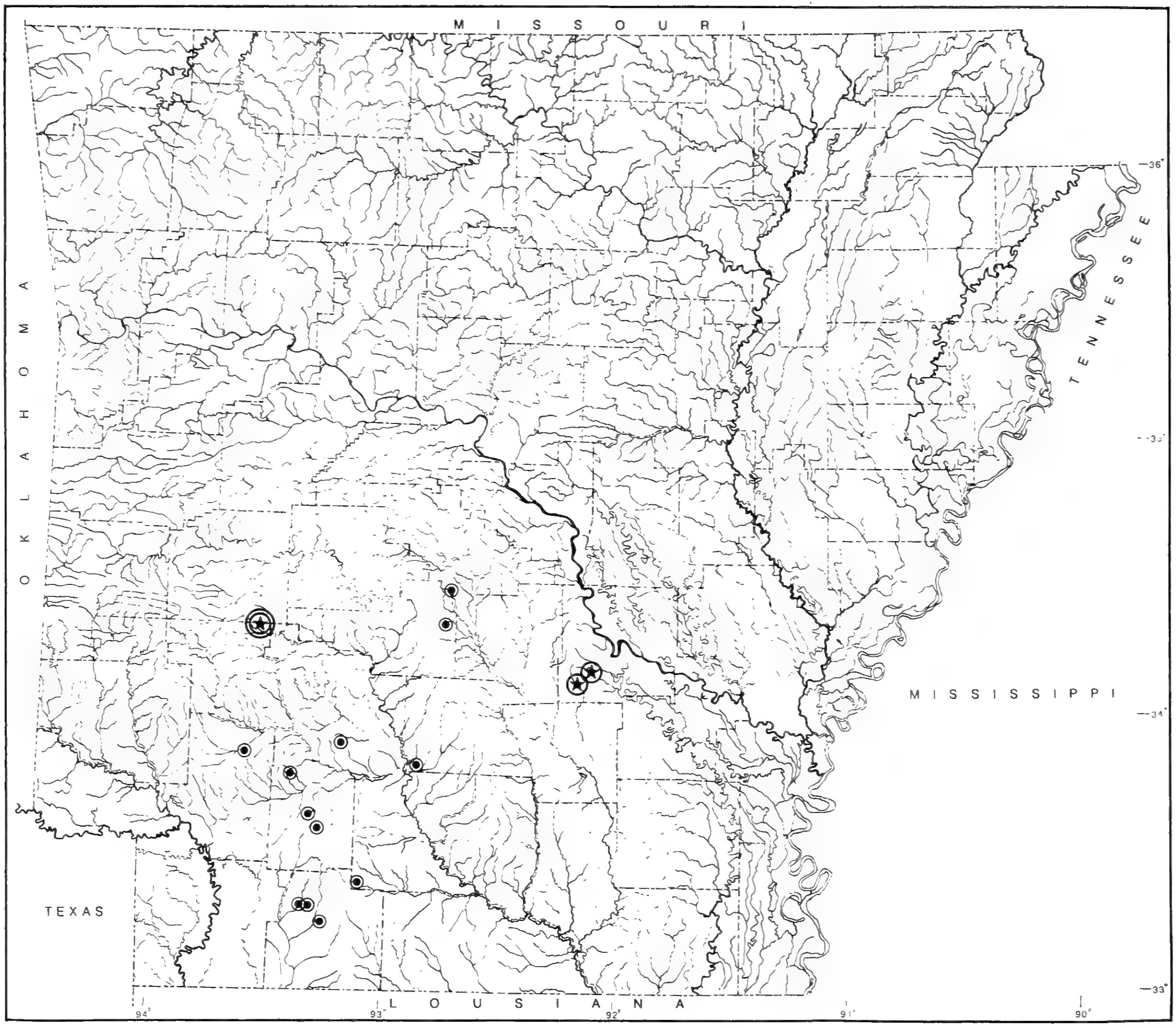

Fig. 5. Distribution of *Fallicambarus* (*F.*) *harpi* (doubly encircled star); *F.* (*C.*) *caesius* (encircled dot); and *F.* (*C.*) *gilpini* (encircled star) in Arkansas. (Some localities listed in text for *F.* (*C.*) *gilpini* are too close to be noted on map.)

chita and Dorcheat Bayou basins in the southern part of the state. We have examined material from the following localities. Clark County: (1) Rose Hedge Cemetery at Gurdon, 1 ♀, 12 Mar 1983, HWR; 1 ♂ II, 1 ♀, Apr 1982, WL; 1 ♂ II, 1 ♀, 3 j♂, 1 j♀, 16 Apr 1983, DDK, HWR. Columbia County: (2) in Magnolia city limits, 1 ♀, 19 Mar 1984, J. Pesses. (3) Waldo, 1 ♀, 24 Aug 1981, EL. (4) seep 0.5 mi (0.8 km) W of Waldo at US Hwy 82, 1 ♀ with young, 17 Mar 1983, HWR. (5) seep 2 mi (3.2 km) W of Waldo at jct of Hwys 82 & 98, 4 ♀, 9 Apr 1983, HWR; 1 ♀, 3 j♂, 1 j♀, 2 ovig ♀, 11 Feb 1984, HWR; 1 ♂ I, 1 ♂ II, 7 ♀, 3 j♂, 3 j♀, 24 Feb 1984, HWR. (6) behind Impson Whitehead Veterinary Clinic in Magnolia, 1 ♂ I, 10 Nov 1979, M. Bryan. (7) Beene residence in Magnolia, 1 ♂ II, 22 May 1983, L. Robison. Dallas County: (8) 0.4 mi (0.64 km) N of Dallas-Ouachita Co line on St Rte 7, 1 j♂, 16 Apr 1983, HWR. Hempstead County: (9) Blevins, 1 ovig ♀, 11 Apr 1984, J. Tucker; 1 j♂, 1 j♀, 20 Apr 1982, EL; 5 j♀, 8 Mar 1984, E. McMullen. (10) Blevins, Sec 15, T10S, R24W, 2 ♀, 15 Mar 1984, B. Scott. (11) Blevins, Sec 11, T10S, R24W, 3 ♀, 15 Mar 1984, T. Taylor. (12) Bollins Bayou near Blevins, Sec 26, T9S, R24W, 1 juv, 25 Apr 1983, HWR. (13) Blevins, Sec 6, T10S, R24W, 1 ♂ II, 2 ♀, 20 May 1983, C. Webb. (14) Blevins, Sec 20, T10S, R23W, 1 ♂ I, 29

Apr 1983, T. Winn. (15) Blevins, Sec 16, T10S, R24W, 1 ♂ I, 2 ♀, 19 May 1983, B. Stephens. Hot Spring County: (16) roadside ditch 2.0 mi (3.2 km) W of Grant Co line on US Hwy 270, 3 ♀, 1 j♂, 30 Apr 1976, HHH & MK. Nevada County: (17) DeAnn Cemetery in Prescott, 2 ♀, 24 Nov 1980, K. W. Williams; 1 ♀, 10 Sep 1979, EL; 1 ♂ I, 16 Feb 1982, KWW; 1 ♂ I, 12 Apr 1980, KWW. (18) 3 mi (4.8 km) E of Rosston on St Rte 4, 2 ♂ II, 4 ♀, 6 j♂, 2 j♀, 8 Mar 1984, DDK. (19) 0.4 mi (6.4 km) from jct of St Rte 19 and Cale Rd, between Laneburg and Rosston, Sec 7, 8, T13S, R21W, 5 ♂ I, 4 ♀, 4 j♀, 15 Apr 1983, DDK. Ouachita County: (20) 0.9 mi (1.44 km) N of jct of US Hwy 79 and St Rte 203, 1 ♂ II, 26 Apr 1986, HWR. Saline County: (21) roadside ditch at Hot Spring County line on US Hwy 67 (Type locality), 1 ♂ I, 2 ♂ II, 1 ♀, 2 j♀ (Type series), 22 Apr 1973, GBH, JEP, HHH.

Color notes.—"(Based on freshly molted holotypic male.) Carapace bluish gray; dorsal thoracic region and large arrow-shaped area (with base between origins of mandibular [adductor] muscles and extending to apex of rostrum) darker and more bluish than lateral surfaces of branchiostegites, hepatic, and posterior gastric regions where more olive than blue. Cephalic section of tergum of first abdominal segment midnight blue, and caudal section slate blue; successive terga also slate blue but becoming progressively lighter in color posteriorly to tip of telson. Second through fifth terga with reticulate, but almost symmetrical, pattern involving oblique sublinear, dorsolateral grayish cream markings. Sixth tergum and telson with ornate symmetrical light markings. Uropods mostly very pale gray, but proximolateral parts somewhat darker with dark bluish splotches and dark median ribs. Antennae and pereiopods with powder blue reticulations. Antennular peduncle dark, antennal peduncle dark mesially and laterally, but broad submedian area of penultimate podomere and lamellar part of antennal scale very pale, lateral margin of scale dark. Cheliped with dorsodistal surface of merus, dorsal surface of carpus, dorsomesial surface of palm, dorsal surfaces of fixed finger, and dactyl powder blue; both fingers with white tubercles on opposable margin and yellowish cream along distal portion; lateral costa cream, and fingers terminating in brownish cornified tips; bluish color on all podomeres fading ventrally to very pale pinkish cream; articular membranes with dark pink suffusion. Dorsal surface of remaining pereiopods blue from merus distally; basal podomeres and ventral surfaces of all pereiopods and sternum cream. Distal end of dorsal side of merus and dorsum of carpus and propodus of third maxilliped with blue reticulations" (Hobbs 1975:27–28).

Size.—The largest specimen is a female from Nevada County having a cl of 31.4 (pol, 27.5) mm. The smallest and largest first form males have corresponding lengths of 21.1 (18.8) mm and 29.5 (26.4) mm, respectively. The smallest female carrying eggs or young has corresponding lengths of 27.2 (24.4) mm.

Life history notes.—First form males have been collected in February, April, May, and November. Ovigerous females were found in February and April; only one, having a carapace length of 28.4 mm, seemed to be carrying anything like a full complement of eggs: 35 with diameters of 2.1 to 2.3 mm; the diameters of the few eggs carried by the other two females were 2.0 or 2.1 mm.

Ecological notes.—In the type locality, this crayfish was collected from highly branching burrows in "rain soaked soil consisting of clay, organic material, and some gravel" (Hobbs 1975:28). As in many, if not most, of the other known localities, sedges and grasses were present in the immediate vicinity of the burrows or nearby, and none was taken from burrows more than one meter deep, most, if not all, of which opened to the surface through two or three chim-

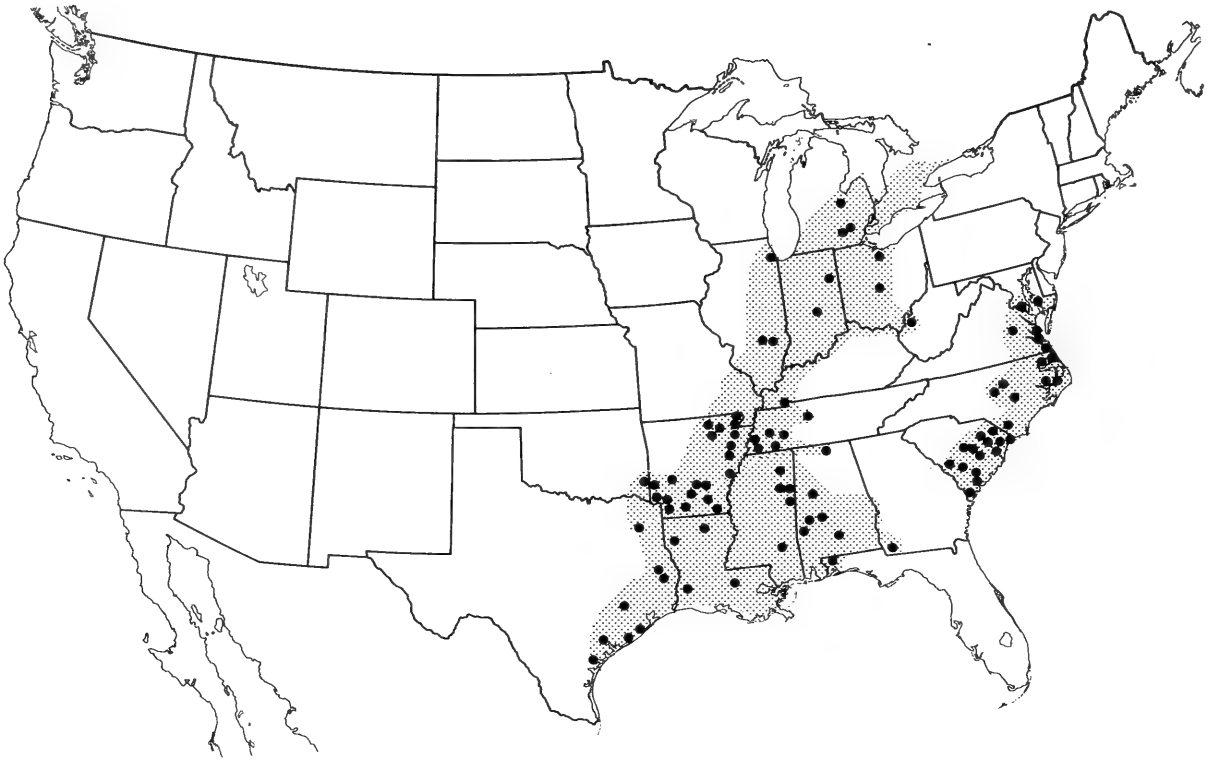

Fig. 6. Distribution of *Fallicambarus* (*C.*) *fodiens*. Dots mark localities represented by at least one first form male.

neys, and occasionally there was an opening to one of the galleries that was not marked by a turret.

Fallicambarus (*Creaserinus*) *fodiens* (Cottle)

Figs. 1*b, o, s, t, u,* 6–9, 10*a–x*

Astacus fodiens (Cottle, 1863:217) [Types: not extant. Type locality: "Upper Canada," probably Ontario.].—Hobbs, 1969a: 111; 1973:463.—Bouchard, 1976b:586.—Page, 1985:422.

Cambarus obesus Hagen, 1870:82 [in part].—Faxon, 1885:71.—Osborn & Williamson, 1898:21.

Cambarus argillicola Faxon, 1884:115, 116, 144; 1885:56, 72, 76–78, 160, 174, pl. IV: fig. 2; 1890:624–625; 1898:650, 690; 1914:391, 400, 424, 426.—Underwood, 1886:366.—Hay, 1891:147; 1896:478, 491–493; 1899:959, 962; 1919:232; 1920: 83.—Stebbing, 1893:208.—Osborn & Williamson, 1898:21.—Williamson, 1899:48.—Harris, 1901:191; 1903a:59, 71–72, 105, 137, 139–140, 142–144, 146, 147, 150–155; 1903b:603, 605, 608.—Ortmann, 1902:277, 280, 283; 1905:120, 123, 136; 1907:712.—Pearse, 1910a:10, 11, 15, 19, 20, pl. VII; 1910b:73; 1911: 130.—Huntsman, 1915:158.—Cahn, 1915:136, 174.—Cummins, 1921:28–30.—Engle, 1926:89, 93, 94, 97, 98.—Turner, 1926:146, 154, 156, 160–163, 168, 169, 178, 186–188, 192.—Creaser, 1931:263; 1932:336.—Lyle, 1937:2, 16; 1938:76.—Brimley, 1938:503.—Bouvier, 1940:71.—Hobbs, 1942:165; 1948: 223, 224, 229, 230.—Rhoades, 1944: 98.—Bovbjerg, 1952:34.—Eberly, 1955: 283.—Crocker, 1957:90.—Hobbs & Hart, 1959:187.—Penn & Marlow, 1959:195.

Cambarus uhleri Faxon, 1884:116–117, 145 [Types: holotype, MCZ 3,624; paratypes, MCZ 3,633, 3,635, 3,636. Type locality: "Swamp on Eastern Road near Felsbury, Somerset County, Maryland" (restricted by Faxon, 1914:426).]. Faxon, 1885:22, 59, 77–78, 160, 166, 173, pl. VIII: figs. 8, 8′, 8a, 8a′.—Underwood, 1886:373.

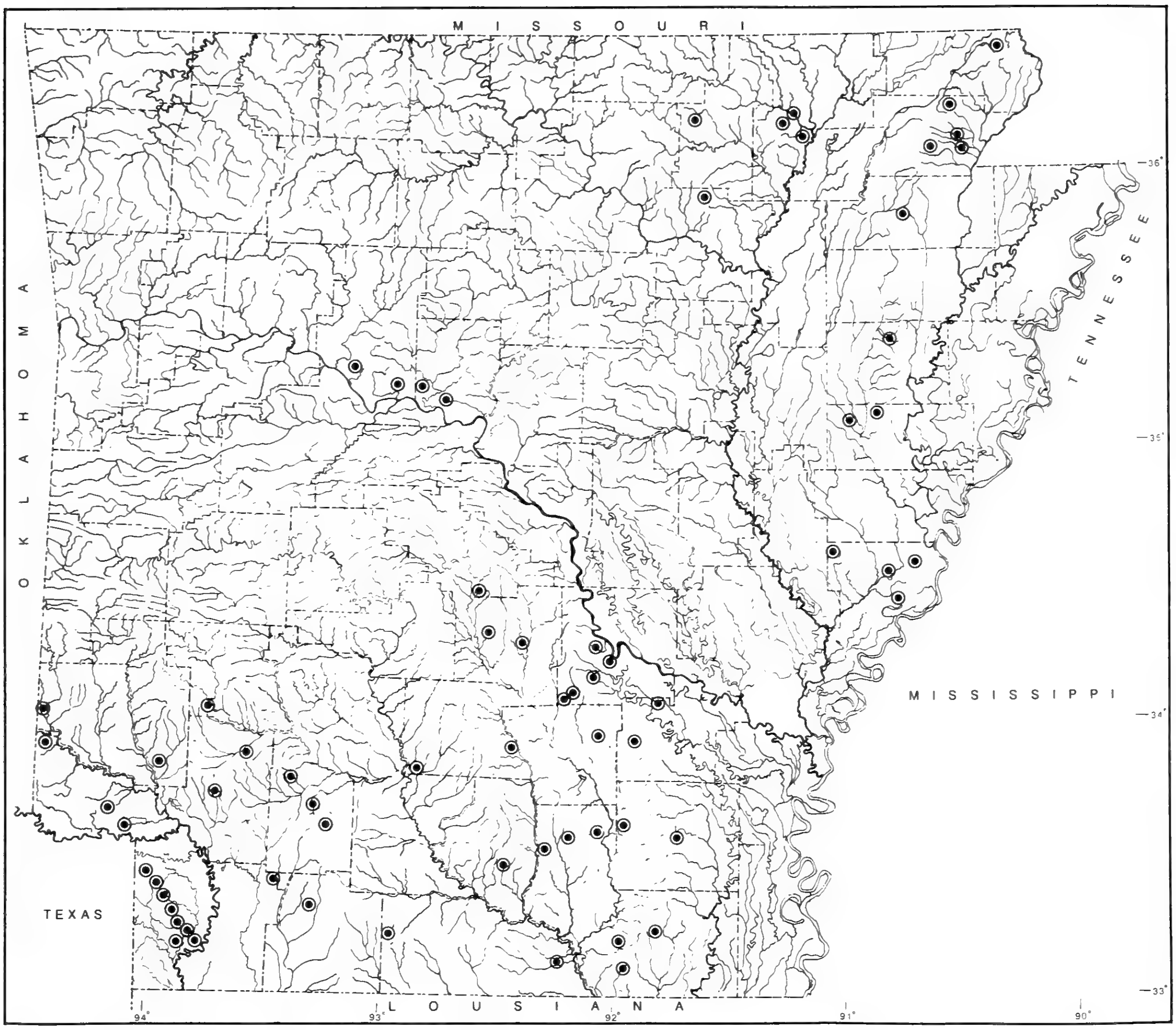

Fig. 7. Distribution of *Fallicambarus* (*C.*) *fodiens* in Arkansas.

Cambarus diogenes.—Faxon, 1885:71 [in part].

Cambarus uhleri.—Hay, 1899:959, 962; 1904:165.—Ortmann, 1902:277, 315; 1905:119, 123, 128.—Harris, 1903a:59, 80, 131, 138, 141, 142, 152, 158; 1903b: 606.—Williamson, 1907:755.—Fowler, 1912:568.—Faxon, 1914:400, 426.—Hay & Shore, 1918:401, pl. 28: fig. 6.—Creaser, 1931:269.—Brimley, 1938:503.—Hobbs, 1942:165; 1948:229; 1955:95, 98; 1959:896; 1966a:68, 70, 71; 1966b:115; 1968:K16; 1981:270.—Penn, 1955:73.—Crocker, 1957:69, 90.—Crawford, 1959: 150, 151, 177.—Meredith & Schwartz, 1959:2; 1960:4, 5, 21, 23, 27, 28, 30; 1962: 2.—Hoffman, 1963:330.—Miller, 1965: 43.—Hobbs III, 1969:42.—Hart & Hart, 1974:73, 91.—Holt, 1973:93.—Pickett & Sloan, 1979:26.—Andolshek & Hobbs, 1986:18.

Cambarus (*Bartonius*) *argillicola.*—Ortmann, 1905:120.

Cambarus (*Bartonius*) *uhleri.*—Ortmann, 1905:120.

Bartonius argillicola.—Williamson, 1907: 749, 752, 755, 758, 762, 763.

Cambarus (*Cambarus*) *uhleri.*—Fowler, 1912:341 [by implication].

Cambarus fodiens.—Huntsman, 1915: 158.—Creaser, 1931:263; 1932:336.—Hobbs, 1941:121; 1942:165, 167; 1948: 223, 224, 226, 229, 230; 1955:95, 98; 1959:896; 1966b:115; 1968:K16.—Penn, 1941:8; 1955:73, 80, 81.—Rhoades, 1942: 3; 1944:98; 1948:18; 1950:2, 3, 5; 1961: 2, 4.—Hobbs & Marchand, 1943:6.—Bovbjerg, 1952:34–36, 40–54; 1970:

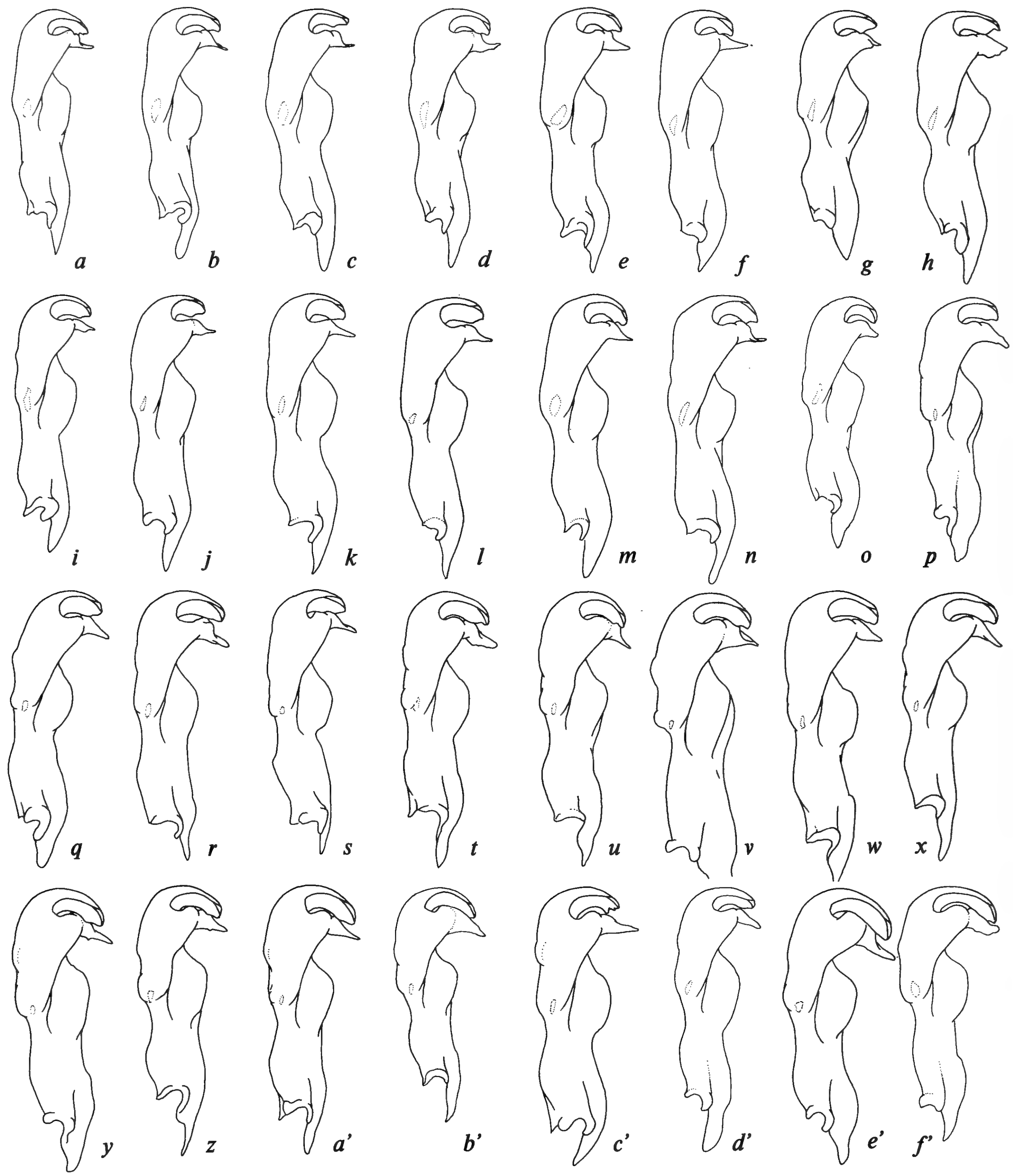

Fig. 8. Mesial view of first pleopods of *Fallicambarus* (*F.*) *fodiens* from following counties in Michigan: a, Saginaw; b, c, Washtenaw. Indiana: d, e, Wells; f, Marion. Illinois: g, Cook; h, Jasper; i, Clark; j, Effingham; k, l, Richland. Ohio: m, Erie; n, Franklin. West Virginia: o, Mason. Arkansas: p, q, Lawrence; r, Sharp; s, Clay; t, u, Greene; v, Craighead; w, x, Independence; y, Cross; z, St. Francis; a′, Phillips; b′, Grant; c′, Jefferson; d′, e′, f′, Dallas.

232.—Pennak, 1953:464.—Eberly, 1954: 59; 1955:283.—Williams, 1954:810, 900, 902, 912, 918.—Spoor, 1955:77.—Crocker, 1957:90.—Penn & Hobbs, 1958: 482.—Hobbs & Hart, 1959:149, 151, 159–161, 164, 169, 171, 185, 187–188, fig. 11.—Hart, 1959:204.—Penn & Marlow, 1959:195, 202.—Wiens & Armitage,

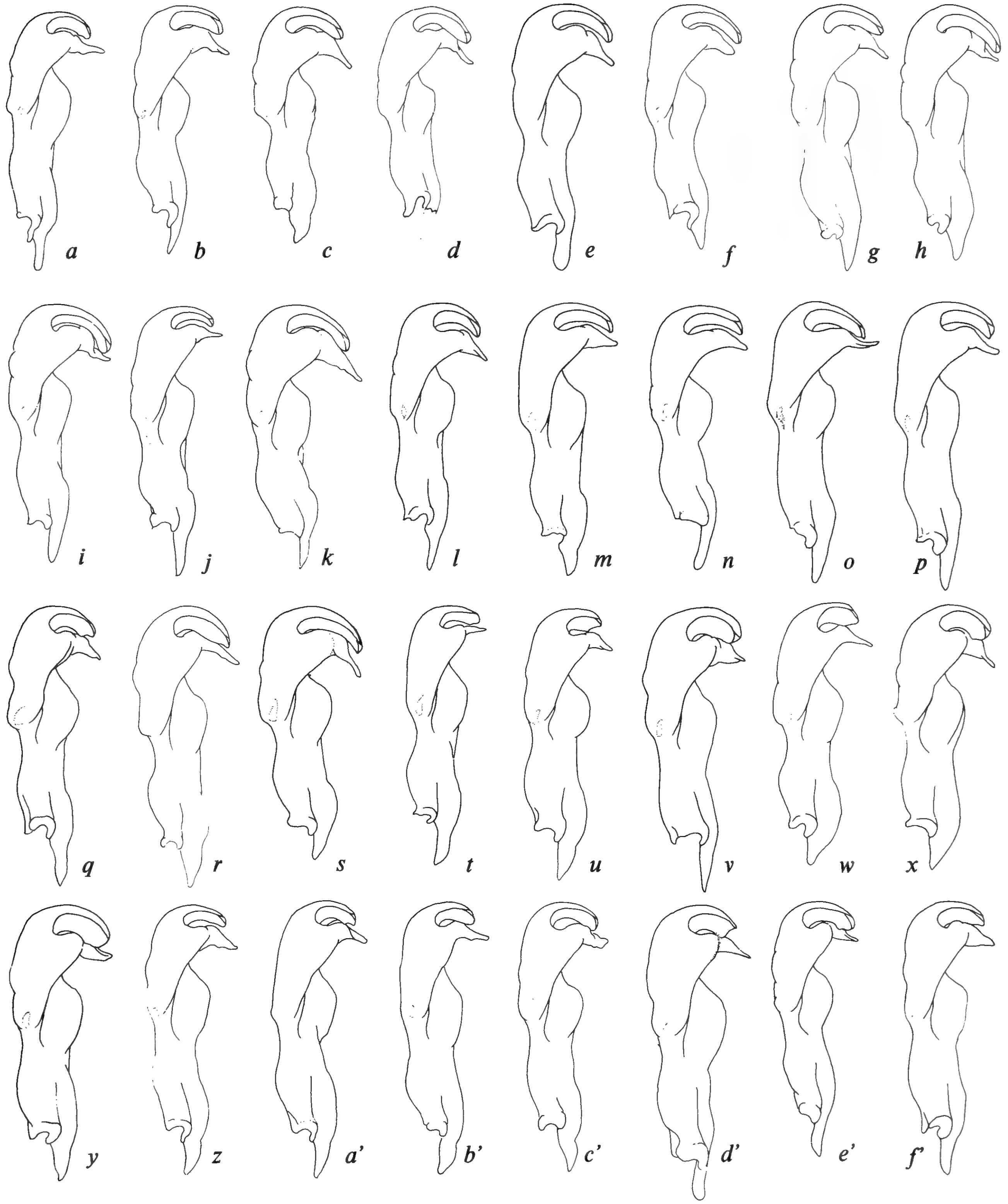

Fig. 9. Mesial view of first pleopods of *Fallicambarus* (*F.*) *fodiens* from following counties or parishes in Arkansas: a, Ashley; b, Bradley; c, Columbia; d, Miller; e, Little River; f, Sevier. Oklahoma: g, McCurtain; Texas: h, Upshur; i, Angelina; j, k, Jasper; l, Brazos; m, Brazoria; n, Madagorda; o, Victoria; p, Aransas. Louisiana: q, De Soto; r, Ouachita; s, Calciseau; t, East Baton Rouge. Tennessee: u, Tipton; v, Crockett; w, Shelby; x, y, Hardeman; z, Cheatham. Mississippi: a', Lee; b', Clay; c', Oktibbeha; d', Lowndes; e', Noxubee; f', Jones.

1961:39–54.—Bowler, 1963:128.—Mobberly, 1965:45.—Judd, 1968:1–4, 6, 8.—Crocker & Barr, 1968:VIII, 12, 15, 29, 33, 35–37, 40, 56, 58–60, 125, 127, 129–135, 139, figs. 28, 37, 46, 57, 62, 85.—Fitzpatrick & Payne, 1968:14.—Jaspers & Avault, 1969:637.—Waywell & Corey, 1970:1462–1464; 1972:294–298.—Bell,

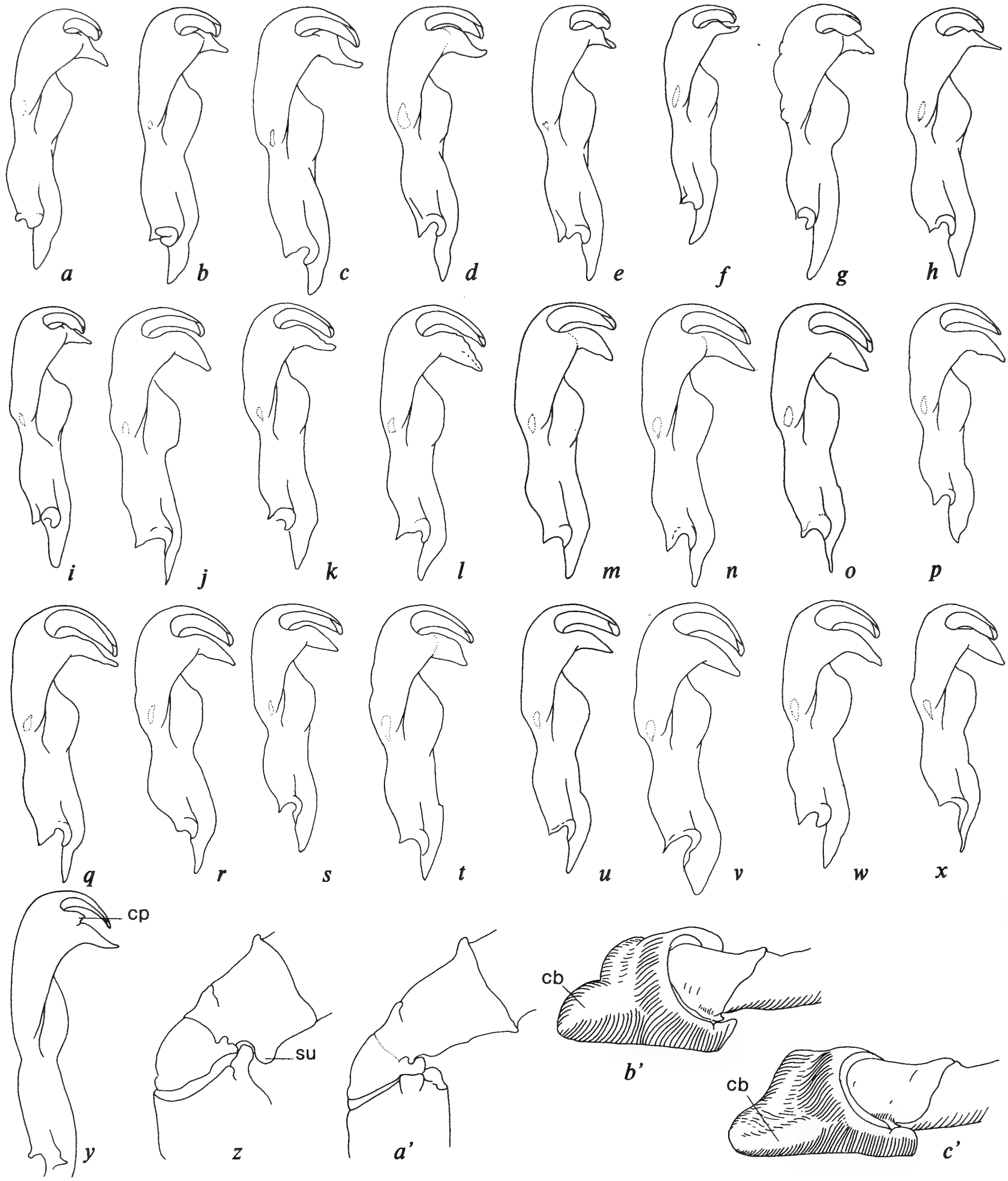

Fig. 10. (All illustrations from first form males.) a–x, Mesial view of first pleopods of *Fallicambarus* (*F.*) *fodiens* from following counties in Alabama: a, Lauderdale; b, Limestone; c, d, Tuscaloosa; e, Perry; f, Choctaw; g, Maringo; h, Butler. Florida: i, Santa Rosa. South Carolina: j, Beaufort; k, Bamberg; l, Colleton; m, Richland; n, Clarendon; o, Dillon; p, Marion; q, Horry. North Carolina: r, Columbus; s, Sampson; t, Hyde; u, Perquimines. Virginia: v, Norfolk; w, Warwick. Maryland: x, Dorchester. y, Same of *F.* (*F.*) *strawni* (cp, cephalic process); z, Lateral view of basal podomeres of cheliped of *F.* (*C.*) *fodiens* (su, sufflamen); a′, Same of *F.* (*F.*) *jeanae*; b′, Basal podomeres of fourth pereiopod of *F.* (*C.*) *burrisi* (cb, coxal boss); c′, Same of *F.* (*C.*) *gordoni* (cb, coxal boss).

1971:17.—Hobbs & Hall, 1974:200.—Terman, 1974:33, 34.—Williams, Williams, & Hynes, 1974:365–369, figs. 1, 2.—Caine, 1974:2.—Becker, Genoway, & Merrill, 1975:384.—Gladwell, Bowler, & Duncan, 1975:89.—Lake, 1977:59.—Berrill, 1978:166.—Momot, Gowing, & Jones, 1978:18.—Radaj, 1978:1.—Reinert, 1978:8.—Lawton, 1979:6.—Pickett & Sloan, 1979:26.—Bousfield, 1979:292.—Crenshaw, Lemons, & Russo, 1980:245.—Grow & Merchant, 1980:234.—Grow, 1981:355.—Kiley & Dineen, 1982:212.—Maude & Williams, 1983:68, 74, 76, figs. 6, 7.—McMahon & Wilkes, 1983:133.

Cambarus (*Bartonius*) *fodiens*.—Creaser, 1931:260, 261, 263, 269–272, fig. 37.

Cambarus hedgpethi Hobbs, 1948:224–230, figs. 17a–f, h–j, l [Types: holotype, morphotype, USNM 85146 (♂ I, ♂ II), and allotype, USNM 85147 (♀); paratypes, USNM. Type locality: lower middle part of Aransas National Wildlife Refuge, Aransas Co, Texas.].—Washburn, 1953:6.—Penn, 1953:74; 1955:73, 80; 1959:8, 14–17, figs. 9, 27, 46, 64, map 9.—Penn & Hobbs, 1958:454, 462, 465, 467, 471, 473, 476–478, figs. 11, 28, 42, 55.—Hobbs, 1959:896; 1966b:115; 1968:K16.—Penn & Marlow, 1959:195–197.—Hobbs & Barr, 1960:13.—Reimer, 1966:14; 1969:50, 51, 53, 60, 61, figs. 2, 39.—Black, 1967:176; 1969:197.—Walls & Black, 1967:60.—Fitzpatrick & Payne, 1968:14, 20.—Walls, 1968:417.—Hobbs III, 1969:19, 21, 26, 49, 64, tab. 2.

Cambarus hedgepethi.—Walls & Black, 1967:60 [erroneous spelling].

Fallicambarus fodiens.—Hobbs, 1969a:111, 112, fig. 20e; 1972:102, 137, figs. 5u, 82b, 83c, 84b, 85b; 1974a:12; 1974b:23, fig. 82; 1976:551, fig. 2d.—Hobbs & Fitzpatrick, 1970:835.—Bouchard, 1972:52, 62, 63, 107; 1976a:14; 1976b:585, 586.—Hobbs & Barr, 1972:9.—Hart & Hart, 1974:30, 31, 128.—Hobbs & Hall, 1974:200, 201, 203.—Page, 1974:99; 1985:335, 336, 341, 343, 344, 350, 353, 422–426, 436, figs. 155–158.—Phillips, 1980:84.—Grow, 1981:355.—Bouchard & Robison, 1981:26, 27.—Huner & Barr, 1981:47; 1984:42.—Berrill & Chenoweth, 1982:199.—Burr & Hobbs, 1984:14, 15, 16.—Norrocky, 1983:3.—Fitzpatrick, 1986:126, 137.

Fallicambarus uhleri.—Hobbs, 1969a:111, 112, fig. 20j; 1972:102, 147, figs. 82a, 83b, 84a, 85a; 1973:463, 480, figs. 3d, 4; 1974b:24, 101, fig. 84; 1976:551, fig. 1a.—Hobbs & Fitzpatrick, 1970:835.—Peters, 1971:100; 1974:74; 1975:7, 22, 23.—Hart & Hart, 1974:22, 28, 33, 73, 129.—Hobbs III, Thorp, & Anderson, 1976:24.—Hobbs & Peters, 1977:6, 9, 12, 13, 19, 20, 21, 33, 43, 46, 49, 53, 54, 60, 61, 62.—Wharton, 1978:50.—Page, 1985:422.—Fitzpatrick, 1986:126, 137, 138.

Fallicambarus hedgpethi.—Hobbs, 1969a:111, 112, 173, fig. 20f; 1969b:335; 1972:102, 147, figs. 82c, 83d; 1974b:23, 100, fig. 83.—Hobbs & Hobbs, 1970:12, 14.—Hobbs & Fitzpatrick, 1970:835.—Bouchard, 1972:56, 62, 63, 107; 1977:11.—Albaugh, 1973:6, 11, 12, 25, 103.—Albaugh & Black, 1973:183, 184, 185.—Payne & Riley, 1974:125–127.—Hart & Hart, 1974:23, 93, 94, 97.—Reimer & Clark, 1974:168, 175, figs. 27–30.—Reimer, 1975:24.—Lahser, 1976:278, 279, 281–284.—Huner, Meyers, & Avault, 1976:150, 152.—Bouchard & Robison, 1981:26, 27.—Huner & Barr, 1981:57, 58; 1984:50.—Rogers & Huner, 1983:79; 1984:37; 1985:23, 24, 26–28, figs. 3, 4, 5.—Burr & Hobbs, 1984:15, 16.—Walls, 1985:193.—Page, 1985:424.—Fitzpatrick, 1986:137.

Fallicambarus (*Creaserinus*) *fodiens*.—Hobbs, 1973:463, 480, figs. 3g, 4.—Bouchard, 1976a:14; 1976b:586.—Clark & Rhoades, 1979:238, fig. 1.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:168, 169, fig. 175.—Thoma & Jezerinac, 1982:136, 137.—Jezerinac & Thoma, 1984:120–124, fig. 1.—Norrocky, 1984:

65.—Page, 1985:335.—Jezerinac, 1986: 178.—Jezerinac & Stocker, 1987:46, fig. 1.—Hobbs III & Jass, 1988:3, 23, 39–43, 141, 142, figs. 30, 31.—Mansell, 1989.

Fallicambarus (*Creaserinus*) *uhleri.*—Hobbs, 1973:463, 480, figs. 3d, 4.—Hobbs & Peters, 1977:6, 9, 12, 13, 19, 20, 21, 33, 43, 46, 49, 53, 54, 60, 61, 62.—Fitzpatrick, 1983:168.—Cooper & Ashton, 1985:9, 10.—Andolshek & Hobbs, 1986: 24.

Fallicambarus (*Creaserinus*) *hedgpethi.*—Hobbs, 1973:463, 480, fig. 4.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983: 169.

P[*rocambarus*] *Fallicambarus fodiens.*—Hart & Hart, 1974:88 [lapsus].

Fallicambarus hedgepethi.—Huner, 1977:11 [photo in color].

Fallicambarus sp.—Huner, 1978:621.

Fallicambarus (*Creserineus*) *fodiens.*—Jezerinac, 1983:5 [erroneous spelling].

Diagnosis.—Ventral surface of merus of cheliped with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of palm of chela. Chela with lateral margin costate to rounded, never serrate, dorsal surface without scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending along at least basal third of finger. Mesial surface of chela of second pereiopod with conspicuous tufts of plumose setae. First pleopod without proximomesial spur and lacking cephalic process; central projection comparatively weakly arched, base not inclined laterally, distal part directed caudally, with or without subapical notch, but never crossing central projection of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod somewhat rounded, neither strongly compressed nor conspicuously protruding ventrally. Mesial ramus of uropod with distolateral spine; distomedian spine premarginal. Telson divided and with spines on anterolateral flank of suture.

Range and specimens examined.—From southern Ontario southwestward to Aransas County, Texas, and southeastward to the Apalachicola Basin, also present in the Coastal Plain and lower Piedmont from Beaufort County, South Carolina, to Somerset and Dorchester counties, Maryland (Figs. 6, 7). Engel (1926:93) recorded it from Lincoln, Nebraska, but this locality is so far removed from any other reported for the species that it must be confirmed. We have examined some 2500 specimens from Michigan (45), Indiana (58), Illinois (42), Missouri (20), Arkansas (420), Oklahoma (13), Texas (223), Ohio (50), West Virginia (2), Kentucky (58), Tennessee (130), Louisiana (29), Mississippi (143), Alabama (207), Florida (14), Georgia (15), South Carolina (451), North Carolina (386), Virginia (209), and Maryland (30).

Color notes.—In this crayfish, there seem to exist two basic colors and three color patterns, with a wide range of variation linking them. Most of the animals that we have seen are either predominantly tan with brown markings or olive-green with dark grayish to brownish green markings. The lighter ventral and ventrolateral areas may be almost white, cream, yellowish, pink, or lavender. Occasionally we have encountered individuals that are predominantly blue.

As for the color patterns, the striped (Fig. 4*c, e*) is the most common. In it, clearly defined longitudinal stripes, that are usually most obvious on the abdomen, make this pattern conspicuously different from the least common concolorous one. The latter is typified by the absence of stripes, splotches, or specks. Decidedly more common than the concolorous pattern is the speckled one (Fig. 4*d*; often the specks and splotches are much more abundant, especially dorsally, than depicted) in which the carapace and abdomen are marked dorsally by specks and irregular dark spots scattered over a lighter background. Paired dorsolateral concentrations of darker pigment, which are often more diffuse than in Fig. 4*d,* on the abdominal terga no doubt represent remnants of the dark stripes that are so conspicuous in the striped pattern. In specimens exhibiting concolorous patterns, which are not illustrated, the dorsum of the cephalothorax is an almost uniform dark brown, green, or blue, fading laterally to cream or very light gray. The abdominal terga, too, are almost uniformly dark brown, green, or blue almost to their junctures with the pleura, which, together with the uropods, are of a much diluted hue of the color of the dorsum.

All three patterns have been observed repeatedly among specimens collected in a single locality, the most recently seen were in a collection from western Sevier County, Arkansas, less than a mile from the Oklahoma line.

Hay (1904:165) remarked that the specimens from Maryland were "a dirty greenish brown, the tips of the chelae alone being somewhat reddish." He reported further that Uhler, who first collected the species in Maryland, related to him the presence of beautiful yellow spots. While we have not observed the latter, we have encountered specimens with cream, yellow, orange, and red tipped chelae, but we have not associated any of these colors with a particular geographic region.

Size.—The largest specimen of this species that we have examined is a first form male from Richland County, Illinois, which has a cl of 42.8 (pol 36.7) mm. The smallest first form male (from Perquimens County, North Carolina) that we have seen has corresponding lengths of 19.5 (16.0) mm. Those of the largest and smallest from Arkansas are 36.4 (32.4), from St. Francis County, and 22.8 (19.2) mm, from Dallas County. Comparable measurements of the smallest female carrying eggs or young that we have seen are 26.5 (22.6) mm; this specimen was collected in Columbia County, Arkansas.

Life history notes.—Considering populations throughout the range of the species, first form males have been collected during every month of the year; ovigerous females were found from January to June and in September, October, and November, and females carrying young from January to April and in September. In Maryland, this crayfish was reported by Hay (1904) to leave its burrows in the spring when it becomes common in ditches and small streams. Finding both first and second form males in September led him to conclude that the transition in males from form II to form I must occur in the late fall.

The data for Arkansas are indeed inadequate; except for a total of 11 members of the species collected in June, July, and November, all of the material from the state available to us was collected during February (11), March (31), April (250), and May 15). Among the collections from the state, there are first form males collected in February, March, April, May, and November, ovigerous females in February, April, and November, and others carrying young in January, February, and March.

The egg complements of three of the ovigerous females appear to be reasonably complete and are as follows: cl 28.2, pol 24.8 mm, 190 eggs; cl 28.2, pol 24.2 mm, 196 eggs; cl 26.5, pol 22.6 mm, 177 eggs. The diameters of the eggs were 1.9 and 2.0 mm.

Ecological notes.—Ecological data that have been recorded pertaining to *F.* (*F.*) *fodiens* were recently summarized by Hobbs III & Jass (1988:41–43). The following discussion is therefore limited to a few recorded observations on the eastern facies of *Fallicambarus* (*C.*) *fodiens* (formerly *F.* (*C.*) *uhleri*) and to those made by us on the presence of this crayfish in Arkansas, where it frequents temporary pools and burrows from the floodplains of the major rivers to the foothills of the Ozark and Ouachita mountains. According to Faxon (1884:117), his *C. uhleri* occurs in "salt marshes, covered twice daily by the tides, and also in brackish and fresh-water ditches. . . ." On the eastern shore of Maryland, Hay (1904:165) found it to be "rather abundant in burrows in low-lying areas not far from the bay but always near ponds or ditches of freshwater. In nearly every case the area selected was in dense pine woods." Hay also learned from local inhabitants of the area that in the spring the crayfish "emerge from their burrows and are common in ditches and small streams." The original collection of the species taken by Dr. Philip Uhler was made partly in water that was distinctly brackish.

In Arkansas, this crayfish is primarily an inhabitant of temporary bodies of water and burrows, although occasionally it ventures into more permanent lentic and lotic habitats. Apparently wherever it occurs in the State the water table must be within range of its burrowing capabilities, for we have no evidence that any members of the species undergo a life-span devoid of periods of what is an apparently voluntary fossorial existence. Whereas we have retrieved a few specimens from burrows that did not penetrate the water table, most were taken from pockets of water in them at depths of 0.5 to 1.5 meters. The external appearance of these burrows is described in the introductory remarks where it was also pointed out that those excavated by members of this species are comparatively simple. Most consist of a subvertical passageway, in clay, sandy clay, or sandy loam, opening to the surface through one or two apertures that may or may not be surrounded by low, for the most part poorly formed, chimneys, and at the fundus of the passageway there is a slight enlargement. Occasionally we have encountered a burrow with a second subvertical gallery leading downward from the main one. With little doubt, these simple I-, Y- or X-shaped patterns reflect, in part, physical features of the environment involving the availability and retention of water. In habitats where there is evidence (based on the presence of hydrophytic plant communities) that during much of the year the water table is close to the surface, this species is largely confined to the marginal areas, and another (e.g., *F.* (*C.*) *caesius* or *F.* (*C*) *gilpini*) dominates, with its shallow, dendritic systems of galleries, the more permanently wet parts of the seasonal seeps. The burrows of those individuals that invade the wetter areas do branch more than those we have regarded as more typical. Clumps of sedges frequently mark the sites of temporary stands of water, and areas in which a not-too-deep retreat of the water table occurs, features that together provide what appears to be the favorite habitat of the species in Arkansas.

Most of the burrows that we have dissected contained a single individual, occasionally one inhabited by a female and a first form male, and sometimes one housing a female with young either clinging to her abdomen or sometimes with young that are presumed to have abandoned their mother. We have no information as to the permanency of habitation of a domocile by an individual. Until the current study of J. Norrocky (manuscript in preparation) involving marking and recapturing members of the species in Ohio, we were almost convinced that a female was a nearly permanent resident of the burrow she occupied, never wandering far away. This assumption was made, at least in part, on the basis of the size of the turrets marking the entrance/s. There can be little doubt that the larger turrets mark the burrows inhabited by the larger females, and there is no question that the more massive chimneys reflect more spacious and deeper domiciles. These observations suggested to us the probability that the older, larger, females had spent a longer time enlarging and reworking their domiciles than had the smaller females and males, probably spending the better part of their entire lives hauling soil pellets to the surface. In light of some of Norrocky's data (personal communication) there is good reason to question our conclusion as to the tenure of an individual in a single lair. While the males must have their own burrow at the time of their presumed biannual molts, there is good reason to believe that when in form I they abandon their burrows, at least temporarily, for sojourns in the domains of one or more females that might be visited. The question as to whether or not they return to their homestead following the breeding season or seek seclusion elsewhere remains unanswered.

Following rains, when pools flood the mouths of the burrows, the juvenile element of the population emerges in numbers and small crayfish may be observed wandering hither and yon, even during daylight hours. An occasional adult also appears in the open water, and, no doubt, many more adults leave their lairs for short forays in the pools at night, but most return to burrows by at least the early morning hours.

We are much puzzled by the paucity of colonies of this crayfish throughout most of the rice-growing areas of the state. Surely when the region was still wooded, and shallow temporary pools were common features of the landscape, numerous colonies of *F.* (*F.*) *fodiens* must have existed between the Arkansas and Mississippi rivers. Now, one must search rather diligently to find even an isolated burrow in much of the area under cultivation. It is understandable that a crayfish might have difficulty in remaining well established in fields that are subjected to the treatment accorded the cultivation of rice, but why should they not be present in the roadside ditches that border these vast tilled and alternately flooded and drained lands? In Cross County, for example, a careful search of the ditches along highways and secondary roads for miles revealed only one colony of this crayfish, though the lawn around one of the churches in Hickory Grove was pitted by scores of burrows that must have been constructed by members of this species. Not only is this crayfish largely absent where it should occur in numbers, but other species (*Procambarus* (*Ortmannicus*) *acutus acutus* (Girard, 1852), *Cambarus* (*Lacunicambarus*) *diogenes* Girard, 1852, and *C.* (*L.*) *ludovicianus* Faxon, 1914) are also encountered infrequently. It seems likely that something associated with the production of rice is affecting adversely the exploitation of the area by crayfishes.

We are further puzzled by our failure to find a single member of this species between the Arkansas and White rivers downstream from Pope County. We do not claim to have exhausted possibilities of the existence of overlooked colonies, but considerable effort has been expended along several routes traversing the area between the two rivers.

Remarks.—United here are three formerly recognized species which for a number of years have presented difficulties to one of us (HHH) in searching for characteristics that might be used in their differentiation (e.g., Hobbs 1959, 1972, 1973, 1981). In preparing an account of the *Fallicambarus* from the Apalachicola basin in his study of the crayfishes of Georgia, Hobbs (1981) assigned the specimens that he had previously identified as members of *Cambarus fodiens* (Hobbs & Hart, 1959:187) to *F. hedgpethi.* But before doing so he had vacillated between assigning them to one of the two and to describing them as new! Had the material subsequently collected in eastern Arkansas and from a number of other localities, as well, been available to him, it is likely that he would have arrived at the conclusions that have been reached in the current study.

Given specimens from the vicinity of the type localities of these three crayfishes, we do not believe that anyone would have difficulty in distinguishing between them: the first pleopod of the first form males of *F. fodiens* exhibits a much shorter central projection than do those of either *F. hedgpethi* or *F. uhleri,* and the latter has an areola that constitutes less than 39 percent of the length of the carapace whereas that of *hedgpethi* is more, and the opposable margin of the dactyl of the chela with two instead of one major tubercle is typical only of *F. hedgpethi*;

too, in the latter the arrangement of the tubercles on the mesial surface of the dactyl of the chela in two well developed rows differs from the usual single well developed row in the other two. The limited known range of *fodiens* when *uhleri* was described from Maryland by Faxon in 1884, and the existing poor concept of the distribution of the two when *hedgpethi* was found in southwestern Texas, gave neither Faxon nor Hobbs reason to question the validity of the seemingly distinctive characters that they chose in naming what we now believe to be peripherally located populations of a single species. These occur at the angles of a large, distorted, triangular range which in Pliocene, and probably in part of Pleistocene, times must have been continuous. The range appears even now to be unbroken except for a gap apparently existing across the southern part of Georgia where members of the subgenera *Hagenides* and *Leconticambarus* of the genus *Procambarus* are probably vicariating for *F. fodiens* (see Hobbs 1981: 317, 348).

Comparisons of the materials from throughout the range of the species have been made, and we have discovered only a few characters (those associated with the first pleopod of the first form male) that are geographically or ecologically restricted to a limited part of the range of the species. The measurements made of the carapace and chelipeds that have been translated into ratios suggest that some local populations are rather distinctive, but they, too, are not consistent for large segments of the range, and there are no indications of clinal trends. Until now, the *Fallicambarus* ranging along the Atlantic versant from South Carolina to Maryland has been identified as *F.* (*C.*) *uhleri.* In southern South Carolina the areola of this crayfish spans from 36 to 41 percent of the carapace length, in North Carolina from 34.8 to 38.7 percent, and in Virginia and Maryland 35.2 to 38.5 percent, and in several localities in South Carolina the ratio is distinctly above 39 percent. When these specimens from South Carolina are compared with others from the state, we find nothing else that will set them apart, and in the midst of their range there are specimens with areolae occupying as little as 36 percent of the carapace length. If the comparisons are extended to specimens from more western localities including those from Arkansas and Texas the ratios range from 32.7 in Cheatham County, Tennessee to 41.5 in Tuscaloosa County, Alabama, and Brazos County, Texas. Moreover, there seems to be no distributional pattern in the variations between these extremes.

Even the three color patterns (concolorous, speckled, and striped) that have been noted appear in a single population. Most of the specimens that we have examined from Illinois to Ohio and West Virginia northward possess chelae in which the opposable margin of the fixed finger bears one tubercle that is slightly to distinctly larger than the others, and the tubercles on the mesial surface of the dactyl are largely aligned in a single row. Specimens from the Atlantic versant exhibit, for the most part, similarly adorned chelae. In contrast, however, in most of those in the lower gulf coastal area, the fixed finger bears two large tubercles and those on the mesial margin of the dactyl form two well developed rows. In eastern Arkansas, Tennessee, and Alabama, these features appear in a haphazard fashion.

First pleopods of first form males from throughout the range of the species are depicted in mesial aspect in Figs. 8–10. On the basis of variations noted in specimens from Ontario (see Crocker & Barr 1968: fig. 28), Michigan, and Ohio to Aransas County, Texas (from Missouri southward only west of the Mississippi River), and were there no populations occurring east of the river, we should not hesitate to conclude that two subspecies of *F. fodiens* should be recognized. The nominate subspecies (distinguishable almost solely on features of the first pleopod of the first form male in which the comparatively short central projection usually bears a subapical notch (Fig. 8*a–y*)) could be considered to occupy the northern sector, extending as far south as northern Arkansas, where throughout the eastern part of the state it intergrades (Figs. 8*z*–9*g*) with the more southwestern populations, ranging from southwestern Arkansas and southeastern Oklahoma southward. These more southern populations exhibit the facies that has been associated with *F. hedgpethi* (recognized by the possession of a long central projection lacking a subapical notch, Fig. 9*h–s*). It should be noted that an occasional influence of the *fodiens* genome surfaces in specimens occurring south of the Arkansas border (see Fig. 9*j, q*). East of the Mississippi River, we fail to find any such regular distribution pattern in the variation of pleopodal features (Figs. 9*t*–10*i*) except along the Atlantic versant from South Carolina to Maryland (Fig. 10*j–x*). But the same type pleopod that characterizes those populations occurring along the eastern seaboard may be found in specimens from Alabama and Texas (Fig. 9*j, t*). Thus, we have been unable to discover a single character that serves consistently to distinguish between the formerly recognized *F.* (*C.*) *fodiens, F.* (*C.*) *uhleri,* and *F.* (*C.*) *hedgpethi.* The two diagnostic features that Faxon (1884:117) mentioned as setting his *Cambarus uhleri* apart from *C. argillicola* (=*F. fodiens*) were its "plane rostrum [and] shape of the hand. . . ." Many specimens, particularly those from the Carolinas, have concave rostra, and while we are not certain as to which features in the "shape of the hand" Faxon was referring, there seems to exist as much variation within specimens from South Carolina to Maryland as we have noted in individuals from the rest of the range of the species, and we have recognized no feature as being unique. As noted above, the same applies to characteristics pointed out by Hobbs as typifying his "*Cambarus hedgpethi.*"

Notes on sex ratio.—In all of the studies of which we are aware that have yielded data on the sex ratios of cambarids except that of Creaser (1934) (e.g., Andrews 1904, Penn 1943, Smith 1953:92, and Smart 1962:94), all have revealed a near 1:1 ratio. Insufficient numbers of individuals of any population of members of the genus *Fallicambarus* in Arkansas have been available that might permit an estimate of the sex ratio in any population, but, in the samples at hand there are many more females than males. Most of our adult specimens of *Fallicambarus* (*F.*) *fodiens* were removed from burrows, and of 293 adults, less than half, only 98, are males. In order to support the belief that our data are little biased, we have repeatedly attempted to discover some way in which to determine whether a burrow to be excavated contains a male, female, or pair, but we have been unsuccessful. (As will become evident below, the importance of obtaining first form males from throughout the range of the species is paramount.) On 21 April 1973, in a seepage area 0.4 mile east of the Oklahoma State line on U.S. Highway 70, in Sevier County, Jean Pugh and HHH removed 23 females from burrows before they found a male. In Phillips County, on 17 April 1985, Robert Gilpin and HHH retrieved females from 14 burrows in one locality without finding a male, and, at another nearby, they unearthed five females before taking a male. Except for their apparent rarity, we are aware of no evidence that the males of *F.* (*F.*) *fodiens* might be more secretive than are the females; and, we suggest that perhaps two of their habits are responsible for the real or apparent absence of half of them (assuming the sex ratio at hatching is near 1:1) from the adult population. To a minor extent, perhaps our data are biased, for the burrows of the males seem sometimes to be less elaborate than those of the female, and this is reflected in the often smaller, open, and eroded turrets marking their domiciles. Admittedly, such burrows offer less temptation to the collector, who, for good reason, prefers to explore one over which the turret is capped, or, if open, adorned with comparatively recently deposited, not abraded, pellets. Well-formed soil pellets offer evidence of the presence of a crayfish instead of perhaps a snake (*Agkistrodon piscivoris* or an ill-tempered *Nerodia sipidon*), an *Amphiuma,* or some other invader. At one time we suspected that of more importance in skewing the apparent sex ratio of adults than failure of collectors to excavate burrows harboring males are the supposed more frequent wanderings of first form males in seeking mates. In their forays from one lair to another, they place themselves in jeopardy of becoming prey to raccoons, skunks, owls, and other predators, and indeed scat from owls and raccoons has been observed to contain fragments of the exoskeleton of crayfishes within the range of the species in Arkansas. Thus by their being more frequently exposed to predators than are females, we reasoned that they are being passively selected, and perhaps effectively so. What significance, if any, attaches to our having observed more carcasses of first form males than females of this species in areas where their burrows are located escapes us.

We had placed considerable confidence in the above suggestions as possible explanations for the apparent skewed sex ratio existing in the adult populations of *F. fodiens* until, on 22 April 1988, one of us (HWR) collected 30 juveniles (cl 5.5 to 11.5 mm) of this species from a pool in the ditch at the locality mentioned above where Pugh and Hobbs had collected in 1973. Twenty-nine of the specimens were females! The question remains as to whether or not the sex ratio at hatching in this species is 1:1, and if it is what factor/s (cannibalism of the perhaps slower growing juvenile males—the male is the smallest of the 30 juveniles) are responsible for the subsequent alteration of the ratio. That our suppositions might well be suspect seem possible when we remembered Creaser's (1934) study revealing possible seasonal changes in populations of the lake- and stream-dwelling *Faxonius* (=*Orconectes*) *propinquus* in which from August to January 66 to 73 percent of the population was female; during the rest of the year the percentage ranged from 43 to 56 percent. Creaser was apparently as puzzled by these data as are we by the information we have on *F.* (*C.*) *fodiens.*

Fallicambarus (*Creaserinus*) *gilpini,* new species
Figs. 1*q,* 5, 11

Diagnosis.—Cheliped with sufflamen; ventral surface of merus with mesial row of tubercles, lateral one never represented by more than two; length of carpus less than or subequal to width of palm of chela. Chela with lateral margin strongly costate, never serrate, dorsal surface lacking scattered tubercles in lateral half, ventrolateral surface with arched row of prominent punctations bearing long setae, opposable margin of dactyl with distinct excision in basal half, mesial margin without tubercles. Mesial surface of palm of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod lacking proximomesial spur, and lacking cephalic process; central projection weakly arched, its base not inclined laterally, its distal part directed caudoproximally with well defined subapical notch, never crossing central projection of corresponding pleopod. Hooks present on ischia of third pereiopods only. Boss on coxa of fourth pereiopod somewhat rounded, not distinctly compressed. Mesial ramus of uropod with distolateral spine; distomedian spine premarginal. Telson incompletely divided, with spine on anterolateral flank of suture.

Holotypic male, form I.—Eyes small but pigmented and with faceted cornea. Body subcylindrical, very weakly compressed (Figs. 4*b,* 11*a,* l). Abdomen distinctly narrower than thorax (7.3 and 10.1 mm). Greatest width of carapace at level about one-third length of areola from cervical groove where subequal to height (10.1 and

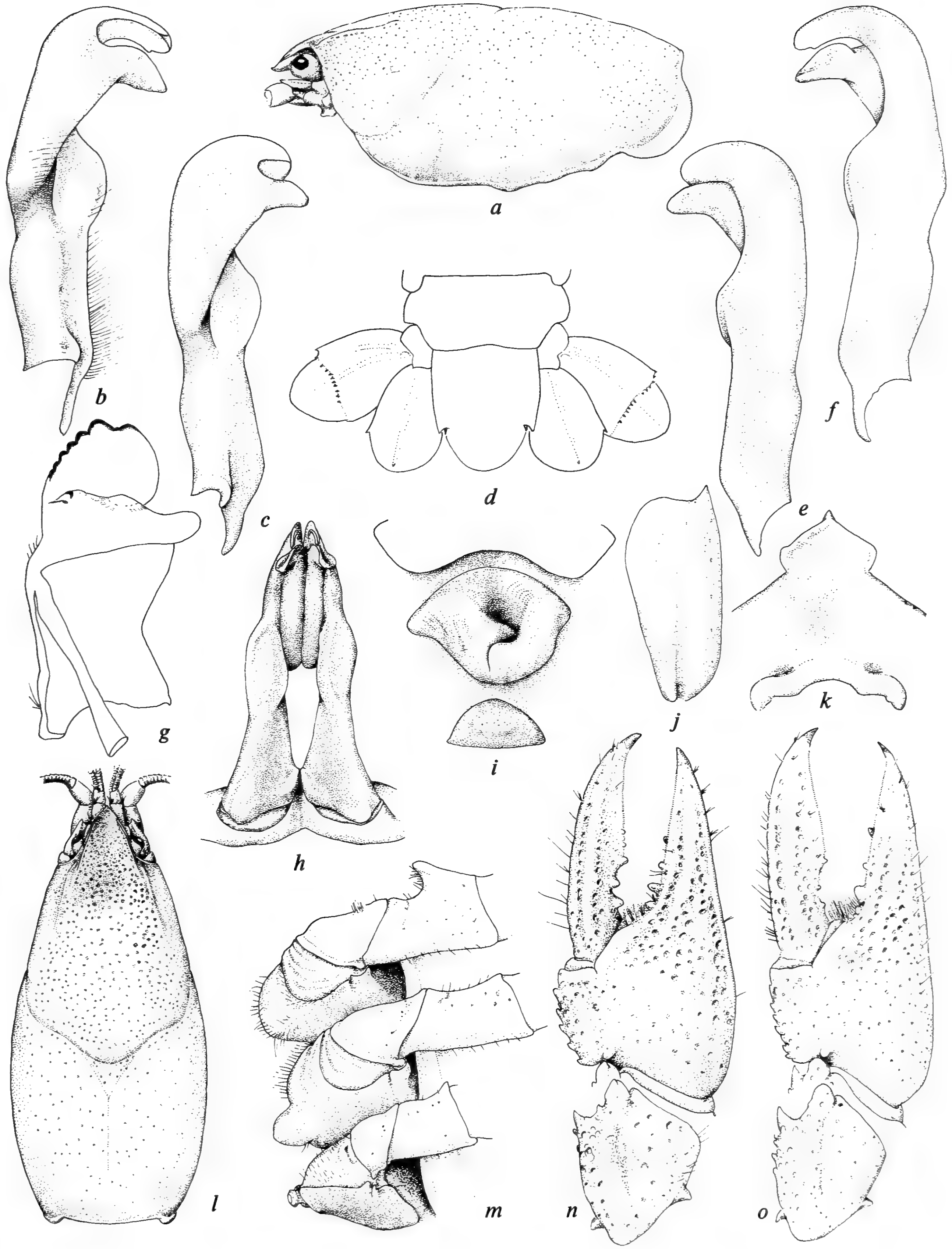

Fig. 11. *Fallicambarus* (*Creaserinus*) *gilpini* (all from holotype except c, e, from morphotype, and i, n from allotype): a, Lateral view of carapace; b, c, Mesial view of first pleopod; d, Dorsal view of caudal part of abdomen; e, f, Lateral view of first pleopod; g, Postaxial view of mandible; h, Caudal view of first pleopods; i, Annulus ventralis and associated sclerites; j, Antennal scale; k, Epistome; l, Dorsal view of carapace; n, Basal podomeres of third, fourth, and fifth pereiopods; n, o, Distal podomeres of cheliped.

10.0 mm). Areola linear over most of length and comprising 40.5 percent of entire length of carapace (46.6 percent of postorbital carapace length). Rostrum with convergent, slender margins gently contracted anteriorly, marking base of poorly delimited acumen, apex corneous, slightly upturned, and reaching base of ultimate podomere of antennular peduncle. Dorsal surface of rostrum concave with submarginal rows of setiferous punctations and others between, especially dense and conspicuous in basal part. Subrostral ridges weak but evident in dorsal aspect to base of acumen. Postorbital ridges slender but well defined and merging almost imperceptibly with carapace above posterior margin of orbit. Branchiostegal and cervical spines absent. Suborbital angle absent, cephalolateral margin of carapace sloping caudoventrally from base of rostrum without excrescence or excision. Carapace comparatively densely punctate dorsally and laterally; row of few small tubercles flanking anterolateral segment of cervical groove.

Abdomen (Fig. 4*b*) shorter than carapace (19.8 and 22.0 mm); pleura small and broadly rounded ventrally, none with angular caudoventral angle; pleuron of first segment clearly overlapped by that of second. Telson (Fig. 11*d*) not divided but deeply incised laterally and caudolateral angles of cephalic section bearing two pairs of spines, more mesial pair smaller and movable. Proximal podomere of uropod with mesial lobe bearing acute angle, lateral one rounded; mesial ramus with distolateral spine and smaller premarginal distomedian spine.

Cephalomedian lobe of epistome (Fig. 11*k*) subtriangular with cephalomedian prominence; cephalolateral margins elevated ventrally and only slightly undulant; main body of epistome depressed but lacking fovea. Ventral surface of proximal podomere of antennule lacking spine. Antennal peduncle without spines, flagellum falling short of caudodorsal margin of carapace. Antennal scale (Fig. 11*j*) small, just reaching base of acumen and penultimate podomere of antennular peduncle; lamella broadly rounded distomesially, broadest distal to midlength, but only slightly wider than thickened lateral part. Mandible (Fig. 11*g*) with cornified subtriangular area of caudal molar process proportionately much smaller than that of *F.* (*F.*) *devastator* and farther removed from corneous tuberculiform cephalic molar process. Ventral surface of ischium of third maxilliped with lateral row of short, plumose setae, and mesial half bearing clusters of longer stiff setae; basis with conspicuous cluster of long setae obscuring proximal part of ischium.

Right chela (Fig. 11*o*) about 2.2 times as long as broad, rather strongly depressed; width of palm about 1.7 times length of mesial margin, latter bearing row of seven tubercles and one prominent one lying slightly dorsal to row between third and fourth from proximal end; irregular row of six much smaller tubercles on dorsal flank of mesial row; dorsal surface of palm and fingers bearing setiferous punctations, those on and adjacent to base of fixed finger and on proximal half of dactyl conspicuous; lateral margin of chela rounded proximally, but largely costate; ventral surface punctate except for single prominent tubercle opposite base of dactyl, ventrolateral arc of punctations, each made prominent by long stiff seta, extending from base of palm to base of distal third of fixed finger. Both fingers with well defined submedian ridge flanked by punctations dorsally; ridges on ventral surface less well defined. Opposable margin of fixed finger with row of four tubercles (third from base largest) along proximal third and one projecting from lower level slightly distal to midlength; single row of minute denticles extending from third tubercle from base to corneous tip of finger. Opposable margin of dactyl with obvious excavation proximally, two tubercles borne on margin of excavation and one marking its distal extremity, all subequal in size; single row of minute denticles extending from distalmost tubercle to corneous tip of finger. Mesial margin of dactyl bearing setiferous punctations, lacking even basal tubercles.

Carpus of cheliped about 1.4 times as long as broad and approximately 1.7 times as long as mesial margin of palm. Dorsal surface with deep submedian longitudinal sulcus flanked by setiferous punctations; mesial surface of podomere tuberculate, that on distal margin acute and much larger than more proximal ones; lateral and ventral surfaces punctate; ventrodistal margin with two acute, corneous tubercles: one on ventrolateral condyle and other mesial to it. Merus with few squamous to rounded tubercles near dorsodistal extremity, two somewhat larger than others; mesial and lateral surfaces finely punctate; ventral surface with mesial row of eight tubercles (nine on left); usual lateral row absent but single tubercle present on left member; lateral row of tubercles characteristic of most crayfishes absent; longitudinal row of long, stiff setae present. Ischium punctate, lacking tubercles ventromesially. Chela of second pereiopod with marginal row of setae on palm, and carpus with dorsal row of long setae; mesial surface of carpus and propodus lacking tufts of plumose setae.

Ischium of third pereiopod only with hook (Fig. 11*m*); latter simple, not overreaching basioischial articulation, and not opposed by tubercle on corresponding basis. Coxa of fourth pereiopod with knoblike caudomesial boss which, if leg extended laterally, projecting mesially. Coxa of fifth pereiopod devoid of boss, ventral membrane setiferous.

First pleopods (Fig. 11*b, f, h*) reaching coxae of third pereiopods and largely hidden by setae extending mesially from ventral margin of sternum. When abdomen flexed, however, apices of terminal elements protruding ventrally beyond setal curtain. Proximomesial spur lacking. Shaft of appendage only slightly bowed, with two terminal elements disposed caudally at about 90 degrees. Mesial process somewhat spatulate, shallowly chamfered, and tilted laterally. Corneous central projection bladelike, with distinct subapical notch, arched and reaching caudally to about same level as mesial process.

Allotypic female.—Differing from holotype in other than secondary sexual characters as follows: acumen not quite reaching base of ultimate podomere of antennular peduncle; postorbital ridges not reaching level of posterior margin of orbit. Abdomen subequal in length to carapace. Distolateral spine on mesial ramus of uropod greatly reduced (perhaps abraded), that on right represented by no more than angle; because of encrustation, dorsal surface of telson and uropods appearing much more strongly setose than that of holotype; both lobes of proximal podomere of uropod rounded. Antennal scale slightly overreaching acumen and base of penultimate podomere of antennular peduncle. Mandible with cephalic molar process strongly abraded, caudal molar process lacking corneous elements. Mesial margin of palm of right chela (Fig. 11*n*) with row of 5 tubercles (left with 6) and row of 4 on dorsal flank (left lacking second row but with single tubercle, between fourth and fifth, ventral to row); dacytl with 2 small tubercles distal to 3 associated with proximal excavation; ischium with ventromesial row of 12 tubercles (11 on left). (See Table 2 for mensural features.)

Annulus ventralis (Fig. 11*i*), 1.5 times as broad as long, situated deeply in sternum; cephalic region immovable, but caudal two-thirds capable of hingelike motion. Sulcus shallow and narrow cephalically, becoming deeper and broader caudosinistrally; high, prominent caudal wall cut by C-shaped sinus arising from fossa at caudosinistral side of sinistrally projecting tongue. Postannular sclerite less than half as long and approximately half as wide as annulus with punctate, oval, ventrally elevated median area.

Morphotypic male, form II.—Differing from holotype in following respects: Tip of

Table 2.—Measurements (mm) of *Fallicambarus* (*F.*) *gilpini.*

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	22.0	24.9	28.3
Postorbital length	19.1	21.7	25.3
Width	10.1	11.6	13.0
Length	10.0	10.9	12.1
Areola:			
Width	—	—	—
Length	8.9	10.0	11.4
Rostrum:			
Width	3.5	3.5	4.2
Length	3.1	3.7	3.9
Right chela:			
Length, palm mesial margin	3.2	3.3	4.8
Palm width	5.4	6.5	7.4
Length, lateral margin	11.8	12.7	15.2
Dactyl length	8.1	8.5	10.1
Abdomen:			
Width	7.3	7.7	9.3
Length	19.8	25.1	25.0

rostrum abraded but acumen reaching midlength of penultimate podomere of antennular peduncle. Postorbital ridges terminating slightly posterior to caudal margin of orbit; lateral surface of branchiostegites granular; telson divided; both lobes of proximal podomere of uropod rounded; main body of epistome with cephalomedian fovea; left antennal scale as in allotype, right with regenerated distolateral spine; right chela with only five tubercles in row on dorsal flank of mesialmost row; opposable margin of fingers armed as in allotype; opposable margin of dactyl of left chela with seven tubercles, four associated with excavation and three distal to it.

Except for terminal elements of first pleopod (Fig. 11*c, e*), no noteworthy differences noted between morphotype and holotype. Mesial process more robust with less conspicuous groove, but projecting caudally much beyond tip of central projection; latter, in addition to being stouter and noncorneous, also lacking subapical notch.

Color notes.—Basic color pale greenish blue, but cephalic region more lavender than blue; rostral margins and postorbital ridges distinctly dark green. Mandibular adductor and posterior part of gastric area lavender with faint greenish suffusion. Lateral cephalic region fading to white ventrally, but with paired small navy blue spots midway between tip of rostrum and caudal extremity of cervical groove and another less well defined pair abutting cervical groove. Thoracic area dark greenish blue dorsally, suddenly changing to white laterally, and at least half of branchiostegite white. First abdominal tergum dark greenish blue, second slightly paler, and third through sixth yet more pale with faint hint of very pale dorsomedian longitudinal stripe; white margin of all pleura partly separated from blue to bluish green tergum by series of short dark greenish blue bars. Telson with cephalic section mostly bluish, caudal section colorless and translucent; lateral section of lateral ramus of uropod pale bluish green, keels of both rami and margins of basal podomere dark greenish blue. Antennules and antennae with lateral and mesial borders of peduncles darker blue than dorsal and ventral surfaces; flagella greenish blue basally fading to pale tan. Cheliped with dorsal surface of distal part of merus, carpus and chela dark bluish green; tips of fingers yellowish with corneous brown tip; ventrolateral part of palm and fixed finger fading to cream; ridges and tubercles on carpus and palm of chela very dark blue. Venter and basal podomeres of remaining pereiopods white; dorsum of merus, carpus, and propodus of second through fifth pereiopods bluish green, dactyl with some blue but more cream to yellowish.

Size.—The largest specimen available is a second form male having a carapace length of 28.8 (postorbital carapace length, 26.0) mm. Corresponding measurements of the smallest first form male were 21.1 and 18.8

mm, and those of the smallest ovigerous female, the allotype, are 24.9 and 21.7 mm, respectively.

Type locality.—Roadside seepage 3.1 mi south of southern junction of State Route 54 and U.S. Highway 79 at junction of latter with Pepperridge Road (T7S, R10W, Sec 19), approximately 11 miles south of Pine Bluff and about 3 miles north of Cleveland County line, Jefferson County, Arkansas.

Disposition of types.—The holotype, allotype, and morphotype (USNM 219511, 219512, and 218944, respectively) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of 1 ♂ I, 1 ♂ II, 8 ♀, 2 juv ♂, 2 juv ♀, 2 ovigerous ♀.

Range and specimens examined.—All of the specimens were collected from burrows in roadside seepages in Jefferson County, Arkansas: (1) type locality, 1 ♂ II, 26 Apr 1986, HWR; 5 ♀, 2 juv ♂, 2 juv ♀, 18 Mar 1987, HWR (two additional juvenile males were maintained in aquaria until they molted to first form, one in late Feb 1988, and the other, the holotype, on 9 or 10 Apr 1988). (2) 0.2 mi S of Pine Bluff city limits, 1 ♀, 11 Apr 1986, HWR, coll. (3) 3.6 mi N of Cleveland Co. line on US Hwy 79, 2 ♀, 7 Nov 1987, B. F. Kensley, HWR, HHH; 2 ♂ II, 2 ♀, 3 ovig ♀, 11 Mar 1988, HWR.

Variations.—Among the adult specimens, the areola constitutes from 38.1 to 40.6 percent of the total length of the carapace, and from 42.1 to 46.6 percent of the postorbital carapace length. Most of the differences noted in the specimens may be attributed to abrasion and to regeneration of chelipeds. The former is reflected in the absence of an upturned tip on the rostrum, reduced and/or truncated tubercles and spines, and broken or missing setae (particularly noticeable on the third maxillipeds of specimens in late intermolt stages). Regenerated chelipeds can usually be recognized by the absence or reduction of the excavation on the proximal part of opposable margin of the dactyl of the chela, but also by the smaller, and frequent increase in number of tubercles on the opposable margins of both fingers. The number of tubercles in the ventromesial row on the merus of the cheliped ranges from 7 to 11, on the mesial margin of the palm of the chela, from 5 to 7 with 0–6 on the dorsal flank; on the opposable margin of both fingers, there are from 4 to 6 tubercles (in one specimen 2, instead of 1, lie at a lower level on the fixed finger). There is no noteworthy variation in the secondary sexual features of the two available first form males, and in the female, the only conspicuous difference observed is the anticipated occurrence of a mirrored image of features of the annulus described in the allotype.

Life history notes.—No first form male has been collected, and the only two available were reared from very small juveniles collected in March 1987. They were maintained in the laboratory in Washington, D.C., and molted to first form in late February and early April 1988. Three ovigerous females were dug from burrows on 11 March 1988: one with carapace length of 22.3 mm carried 18 eggs along with several empty "capsules," another with cl of 24.9 mm, 20 eggs, and the third with cl of 25.5 mm, 35 eggs. All of the eggs were about 2 mm in diameter. The two juvenile females collected on 18 March 1987 have carapace lengths of 11.9 and 12.1 mm, and the two juvenile males, 11.4 and 11.9 mm.

Ecological notes.—This crayfish has been found only in complex burrows consisting of branching galleries, several of which, except in dry seasons, reach the surface, some of their openings marked by rather crudely constructed turrets. Where *Fallicambarus* (*C.*) *gilpini* has been collected in the same locality with *F.* (*C.*) *fodiens,* the burrows of the former were frequently, if not usually, situated higher on the seepage slope, suggesting that like the partitioning of a habitat in South Carolina by *Cambarus* (*J.*) *carolinus* (Erichson, 1846) and *Distocambarus* (*Fitzcambarus*) *carlsoni* Hobbs, 1983 (see latter, page 437), *gilpini* might prefer areas in which the groundwater is moving, whereas *fodiens* more frequently occurs in areas in which the water is more static. In general, the burrows of *gilpini* are more complex, exhibiting more subhorizontal galleries than do those of *fodiens* that we have excavated in Arkansas.

Relationships.—Fallicambarus (*C.*) *gilpini* has its closest affinities with *F.* (*C.*) *caesius.* In addition to the many features the two species share in common, including being the only typically blue members of the genus, they are the only ones that lack a ventrolateral row of tubercles on the merus of the first cheliped. The most readily observed features that distinguish the two species are the absence of tubercles on the mesial surface of the dactyl of the chela and the presence of a distolateral spine on the mesial ramus of the uropod in *F.* (*C.*) *gilpini.*

Etymology.—This crayfish is named in honor of our mutual friend Robert H. Gilpin, of Cumberland, Maryland, in token of his interest and assistance in collecting much of the material we have from the eastern part of Arkansas.

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SANQUERUS, A REPLACEMENT NAME FOR *POSIDON* HERKLOTS, 1851 (CRUSTACEA, DECAPODA, PORTUNIDAE)

Raymond B. Manning

Abstract.—*Sanquerus* is proposed as a replacement name for the preoccupied portunid genus *Posidon* Herklots, 1851, and the name is removed from the synonymy of *Portunus* Weber, 1795. *Sanquerus* is a monotypic genus containing only the West African *Sanquerus validus* (Herklots, 1851).

Manning & Holthuis (1981:104, 105) pointed out that the West African "*Portunus validus* shows little similarity to any of the many Indo-West Pacific species of the genus, and it shows little affinity with any of the American species of the genus. . . ." They also enumerated differences between *Portunus validus* and *Portunus pelagicus* (Linnaeus, 1758), the type species of *Portunus.* I take this opportunity to remove *Posidon* from the synonymy of *Portunus* and to propose a replacement name for it.

Sanquerus, new name
Figs. 1–2

Posidon Herklots, 1851:3. [Invalid junior homonym of *Posidon* Illiger, 1801 (Crustacea). Type species: *Portunus* (*Posidon*) *validus* Herklots, 1851, by monotypy. Gender masculine.]

Diagnosis.—Size very large, carapace widths in adults exceeding 20 centimeters. Carapace wide, breadth about two times

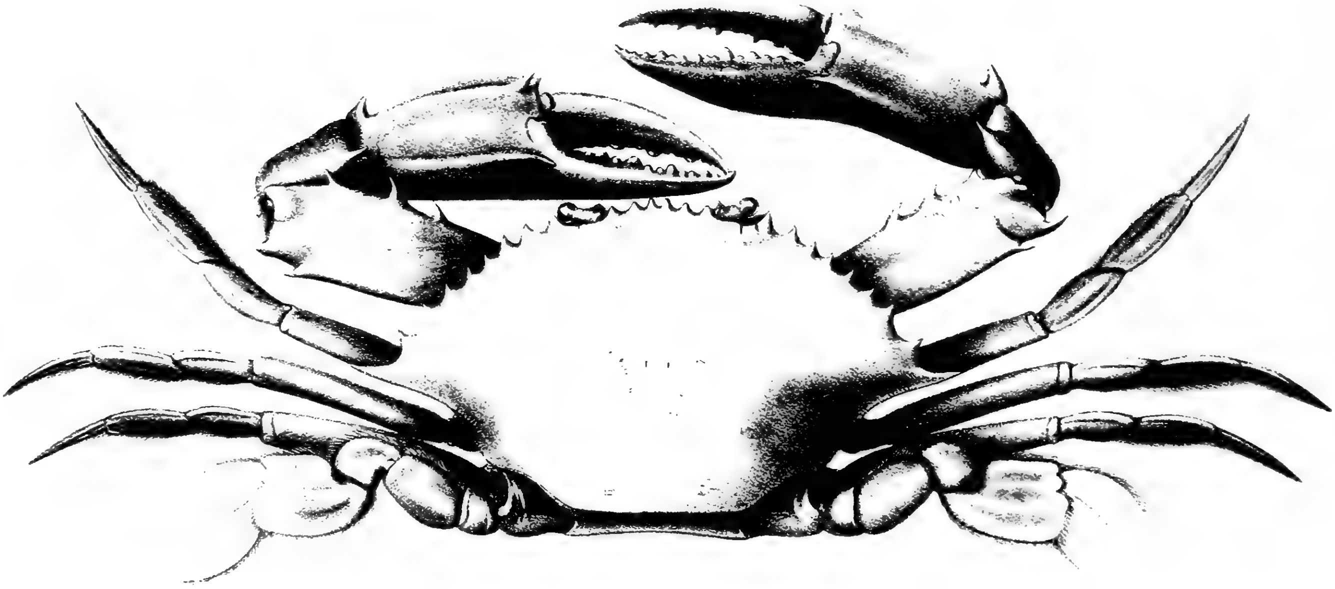

Fig. 1. *Sanquerus validus* (Herklots) (from Milne Edwards 1861, pl. 29, fig. 1).

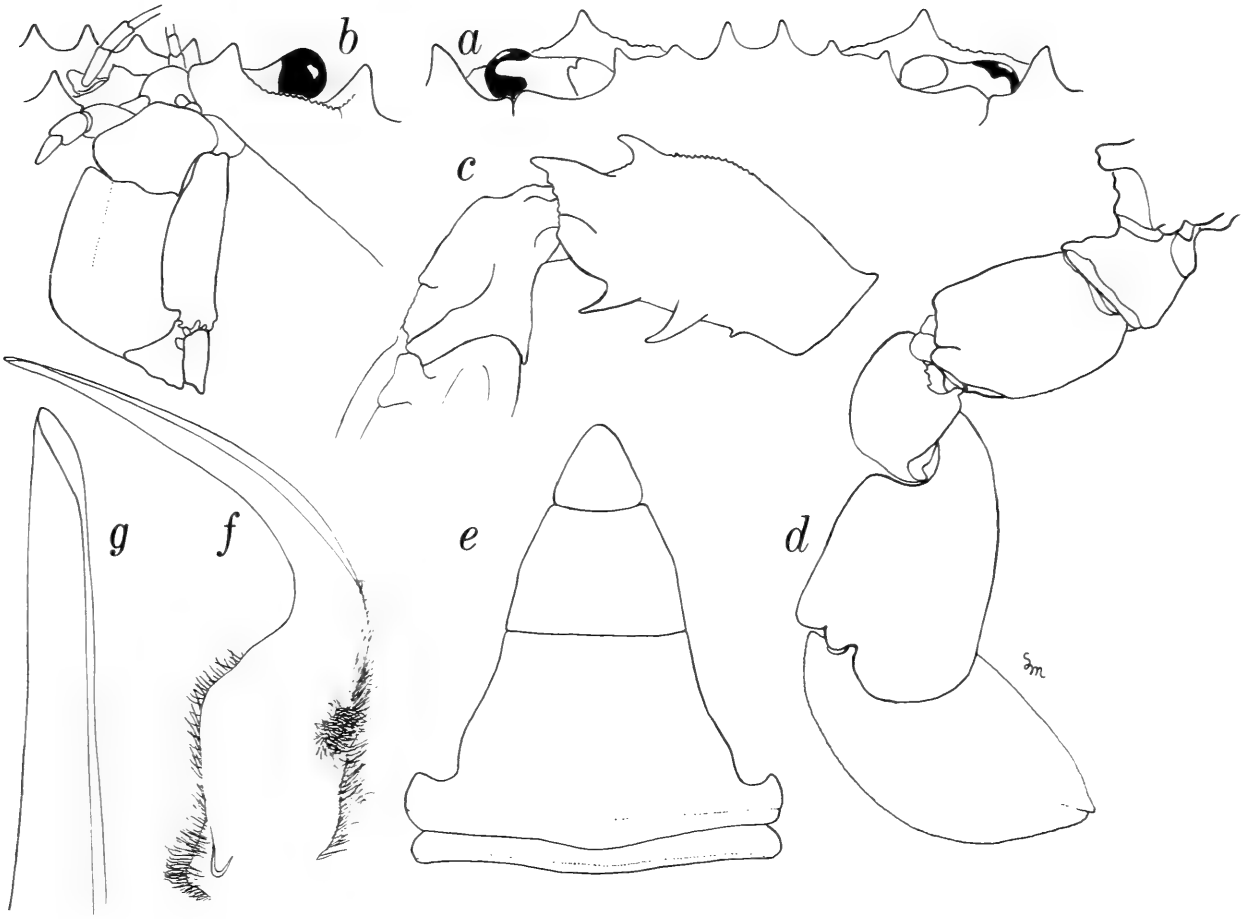

Fig. 2. *Sanquerus validus* (Herklots). a, front; b, third maxilliped; c, merus and carpus of cheliped; d, fifth leg; e, abdomen; f, gonopod; g, apex of gonopod. (a, b, d–g from male, 151 mm wide, Nigeria, USNM 121034; c from male, 61 mm wide, Liberia, USNM 97864) (c, f, g from Manning & Holthuis 1981).

length. Surface of carapace minutely tuberculate, appearing smooth to the naked eye, evenly convex, lacking distinct grooves or ridges, except for ridge extending across posterior margin between bases of last walking legs; posterolateral angles of carapace unarmed; conspicuous white spot present posterolaterally on each side. Front with three pairs of spiniform teeth, including inner orbitals, median pair largest. Interantennular projection low, not visible in dorsal view. Anterolateral margin of carapace with nine spiniform teeth, lateralmost largest. Antenna with free access to orbit. Palate with longitudinal ridge. Merus of third maxilliped lacking produced anterior lobe. Cheliped robust; merus with two posterior spines, one subdistal, three inner spines, and one smaller vental spine distally; carpus with inner and outer spine; palm prismatic and costate, with proximal spine at articulation with wrist, distal dorsal spine, and smaller distal spine on inner carina. Merus of fifth leg with posterodistal margin unarmed, rounded; swimming paddle notched distally. Abdomen of male triangular, 5-segmented, third to fifth segments fused; terminal segment longer than broad. Male pleopod stout, curved laterally, unarmed.

Etymology.—This name is in recognition of the enormous contribution made to the knowledge of the West African fauna by Mr. Robert Sanquer of Vouhé, France, former Trawling Master for the Guinean Trawling Survey. The gender is masculine.

Remarks.—*Sanquerus* is a very distinctive portunid, easily distinguished from all known portunid genera by the smooth, unornamented carapace in combination with the prismatic and costate chelae. It keys to *Portunus* in Rathbun (1930:13), Crosnier (1962:34), Garth & Stephenson (1966:10), and to the couplet containing *Portunus* and *Scylla* in Stephenson (1972:8).

Sanquerus validus keys to *Portunus pelagicus* in Stephenson & Campbell (1959: 90) and to the couplet containing *P. pelagicus* in Crosnier (1962:42). It keys to *Portunus convexus* de Haan, 1833 in Stephenson (1972:13) because of the paired white spots on the carapace, but that species has distinct ornamentation on the carapace and only one posterior spine on the merus of the cheliped. On morphological grounds it keys to the couplet containing *Portunus pelagicus* in Stephenson (1972:15). It differs from *Portunus pelagicus* in numerous features, some of which were mentioned by Manning & Holthuis (1981:105): the carapace lacks surface sculpture and is minutely rather than distinctly tuberculate; the submedian frontal teeth are the largest of the frontal teeth; the interantennular spine is not visible in dorsal view; the third maxilliped extends far less forward; the cheliped is more massive, and the merus is ornamented with two strong posterior spines; the abdomen of the male is broader; and the gonopod is much stouter. As in *P. pelagicus,* the dactylus of the fifth leg is notched distally, not produced into a spine, and the anterior eight anterolateral teeth of the carapace are not alternately large and small.

Sanquerus resembles the Indo-West Pacific genus *Scylla* de Haan, 1833 in having a relatively smooth carapace, but differs from *Scylla* in having the chelae prismatic and costate; in *Scylla* the chelae are robust and smooth (Stephenson & Campbell 1960: 111; Stephenson 1972:8, 44).

In frontal view, the carapace of *Sanquerus* shows very low paired swollen prominences on the protogastric, mesogastric, and mesobranchial regions, and distinct but small paired branchial lobes.

Sanquerus validus is a commercial species occurring off the West African coast, from Senegal to Angola. References to the species may be found in Monod (1956:196) and Manning & Holthuis (1981:103).

Acknowledgments

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RECTIFICATION OF *HALIRAGES REGIS* AND *H. HUXLEYANUS* (CRUSTACEA: AMPHIPODA), FROM MARINE ANTARTICA, WITH DESCRIPTION OF A NEW GENUS, *AUSTROREGIA*

J. L. Barnard

Abstract.—*Halirages huxleyanus* and *H. regis* are removed to the new antarctic genus, *Austroregia.* This leaves *Halirages* with 6 species entirely confined to arctic waters. *Austroregia* is a perplexing genus because it is furnished with calceoli of the same kind found in *Chosroes* and *Gammarellus*; a family Gammarellidae is available for these two genera which would be removed from such families as Eusiridae, Pontogeneiidae and Calliopiidae, in which the genera would have been classified previously. Problems remain on speciation within *Austroregia.*

Halirages huxleyanus (Bate) and *H. regis* (Stebbing) are improperly placed in *Halirages* and are removed to a new genus *Austroregia. Austroregia huxleyana* possesses distinctive calceoli of a kind also present in *Gammarellus, Chosroes* and *Gondogeneia,* adequate to justify the resurrection of the family Gammarellidae within the superfamily Eusiroidea. This reinforces the discovery by Lincoln & Hurley (1981:111) that both the high arctic and high antarctic contain taxa with common ancestry in the gammarellid group, a family first raised by Bousfield (1977), but soon after merged within the family Calliopiidae.

Gammarellidae, revived

Diagnosis.—Characterized by a type 6 calceolus of Lincoln & Hurley (1981) in which the proximal element forms a discrete cup separated from the small 2 to 3-plate distal element by a second smaller cup-shaped element (Fig. 1). Also unique is the arrangement of the calceoli in transverse rows that extend all around the distal margin of the flagellar articles.

Remarks.—The family Gammarellidae was established by Bousfield (1977) to contain two carinate genera, *Gammarellus* Herbst and *Weyprechtia* Stuxberg, separated from other kinds of pontogeneiids by a combination of characters that included a well developed accessory flagellum, lanceolate weakly setose third uropods, and laminar, apically emarginate telson. However, the distinction from other eusiroids was far from clear-cut and in a later updated and revised version of his classification, Bousfield (1983) synonymized the Gammarellidae with the Calliopiidae.

The present use of calceolus morphology and arrangement as a shared apomorphy to resurrect the Gammarellidae produces a family of quite a different complexion. Brought together are four eusiroid genera, *Gammarellus, Gondogeneia, Chosroes,* and *Austroregia,* that would not have been recognized as belonging to a natural and independent group on the basis of traditional morphological characterizations. Thus, *Gammarellus* possesses a well developed multiarticulate accessory flagellum which is at best small to vestigial in *Gondogeneia* and

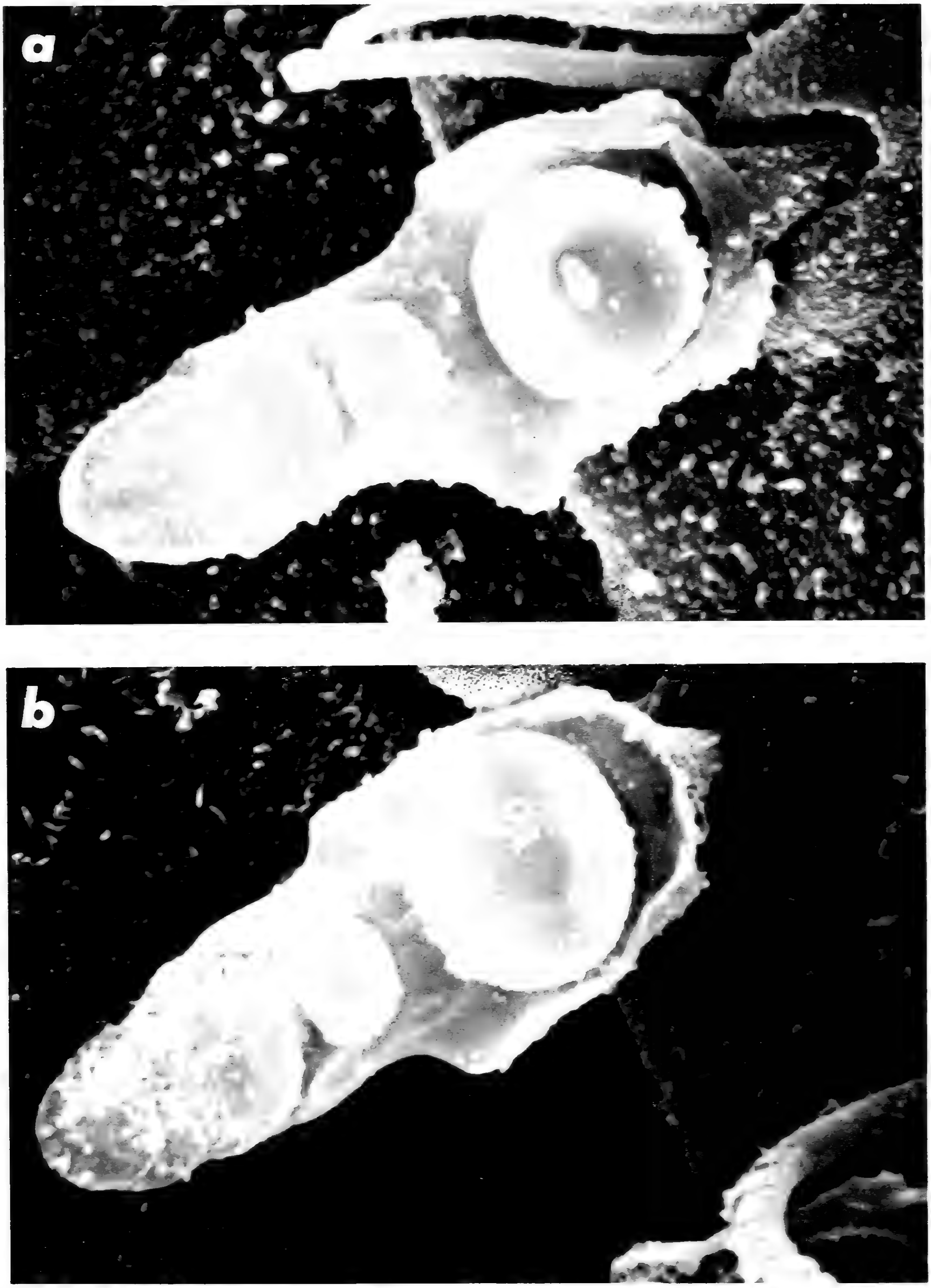

Fig. 1. Calceoli: *a, Austroregia huxleyana,* holotype "a"; *b, Chosroes decoratus.* Magnifications unknown; courtesy of Dr. Roger J. Lincoln.

Austroregia and absent in *Chosroes.* Further, *Gammarellus* is the only member having a coxal gill on pereonite 7, a lobate carpus on gnathopods 1–2, and facial setae on the inner plate of maxilla 2. The telson of *Chosroes* and *Gammarellus* is weakly emarginate, but has a short to moderate cleft in *Gondogeneia* and *Austroregia.* A lanceolate setose uropod 3 is shared by all four genera but is also widespread outside the group.

The single feature uniting the family is the type 6 calceolus. This could be treated as yet another instance of convergence, as has to be argued for many eusiroid characters, but in view of the marked complexity of the calceolus sensory receptor and its novel distribution on the antennal articles, there is adequate justification for recognizing the group as a separate unit within the Eusiroidea.

There is a superficial resemblance of the gammarellid group to the Pleustidae, but the latter family has distinctive labia bearing outer lobes tilted across fused inner lobes; pleustids lack calceoli and further relationships cannot be struck. The lower lip of *Mesopleustes* and *Chosroes* bridges the gap between the two groups.

Families based entirely on calceolar structure are very difficult to handle by taxonomists because many species and genera that obviously are analogous to the calceoliferous members of various families have lost their calceoli. This has been a major problem with Crangonyctidae and will be a problem with Gammarellidae. Only 18 out of 91 families of Gammaridea have one or more species with calceoli. Fortunately, 16 out of the 18 families can be recognized by characters other than calceoli. At best the two families here mentioned are "ghost families" for the identificatory taxonomist because not all of their species and genera are recognizable by ordinary morphological characters. Just as with the Crangonyctidae, there may be species lacking calceoli which are descendants of an ancestor common to the known members of Gammarellidae. For the moment, those species, plus all other members of Eusiridae, Calliopiidae and Pontogeneiidae have to remain in a pool that is identifiable through laborious keys that contain little relationship to the phylogenetic positions of their genera. This is another case of the difference between practical classification involving the identification of species and genera versus phylogenetic classification where species and genera may be arranged on the basis of characters not readily available from preserved museum specimens.

Austroregia, new genus

Type species.—*Atylus huxleyanus* Bate, 1862, here selected.

Etymology.—From "austro," southern, and "regia," kingly.

Diagnosis.—Eusiroid-like amphipods with type 6 calceolus; body carinate; rostrum small; eyes circular; basal article of flagellum on antenna 1 not elongate; antenna 2 as long as antenna 1; upper lip entire; inner lobes of lower lip absent; inner plate of maxilla 1 with only six or fewer setae, mostly terminal; palps disymmetrical or not (type); inner plate of maxilla 2 with only medial setae, none facial; outer plate of maxilliped of basic form and size; gnathopods small, carpus shorter than propodus, nonlobate, gnathopod 1 slightly larger than 2; pereopods 3–4 with nonlobate basis; coxa 4 excavate or not posteriorly; gills unpleated, gill 7 lacking; at least pereopod 7 elongate; outer rami of uropods 1–2 shortened; peduncle of uropod 3 slightly elongate, rami extending equally, poorly setose; telson elongate, cleft about 10–20 percent of its length.

Composition.—*Austroregia huxleyana* (Bate, 1862) and *A. regis* (Stebbing, 1914).

Relationship.—Differs from the confamilial genera, *Gondogeneia* in the presence of large dorsal carinae on pereonite 7 and pleonites 1–3; *Chosroes* in the enlarged gnathopod 1, broader outer plate of the maxilliped and the lack of an anterior lobe on the basis of pereopods 3–4; *Gammarellus* in the nonlobate carpal articles of gnathopods 1–2, lack of coxal gill 7, vestigial accessory flagellum, nonpleated gills, absence of facial setae on the inner plate of maxilla 2, poorly setose inner plate of maxilla 1, and cleft telson.

In addition to the type 6 calceolus, *Austroregia* differs from the eusiroid genera, *Halirages* in the fewer setae on the inner plate of maxilla 1, the lack of facial setae on maxilla 2, and the enlarged gnathopod 1; *Cleippides* in the short carpus of the gnathopods; *Haliragoides* in the lack of inner lobes on the lower lip, the fewer and nonfacial setae of maxillae 1–2 and the regular sized uropod 3; *Whangarusa* Barnard & Karaman (1987), in the carinate body, poorly setose maxillae, and lack of inner lobes on the lower lip; *Paracalliopiella* in the elongate telson, and nonreniform eyes; *Cleonardopsis* in the lack of inner lobes on the lower lip, and lack of carpal lobes on the gnathopods; *Harcledo* in the carinate body, longer anterior coxae and weakly cleft telson; *Amathillopsis* in the vestigial accessory flagellum, nonlobed carpus of the gnathopods, slightly enlarged gnathopod 1, fewer setae on the inner plate of maxilla 1 and the smaller dactyl of the maxilliped; *Meteusiroides* in the carinate body, nonreniform eyes, nonelongate article 1 on the flagellum of antenna 1, nonlobate carpus of the gnathopods, and poorly cleft telson; from *Paramphithoe* in the broader articles 5–6 of the gnathopods, especially the more inflated article 6, the nonbifid coxa 4, the enlarged gnathopod 1, the confinement of body teeth to the dorsal midline and the fewer setae on the inner plate of maxilla 1; from *Pontogeneia* in distinctive calceoli, poorly cleft telson, absence of inner lobes on the labium, enlarged setae on inner plate of maxilla 2 which are fully marginal (versus facial) and the bluntly rounded anteroventral margins of the anterior coxae; and finally, *Calliopius,* in the nonlobate carpus of the gnathopods, nonreniform eyes, absence of inner lobes on the lower lip, and the distinctive calceoli.

Coxa 4 takes different forms. In juveniles it is usually excavate weakly and because in some adults it curls outward it seemingly is deeply excavate when illustrated without flattening. In some large adults this coxa assumes a diamond-shape (Fig. 6*d*).

Presence of calceoli is vagarious. Generally, adults of *A. huxleyana* bear calceoli but most of *A. regis* do not. We have in hand several adults of *A. huxleyana* without calceoli and Stebbing (1888: pl. 73) shows an adult of *A. regis* with calceoli. This fits the vagarious occurrence of calceoli classically known in many species of amphipods where presence or absence occurs at a demal level.

Note on other species.—*Atylus? batei* Cunningham, 1871, from Magellan Strait, apparently is neither of the species studied herein as it has five dorsal body teeth, whereas the two discussed herein have four or fewer.

Austroregia huxleyana (Bate)
Figs. 2–4

Atylus Huxleyanus Bate, 1862:135, pl. 25, fig. 4.—Cunningham, 1871:498.

Acanthozone Huxleyana.—Della Valle, 1893:612, pl. 59, fig. 23.

Halirages Huxleyanus.—Stebbing, 1906: 291; 1914:362.—Schellenberg, 1931:176, pl. 1, fig. k.—K. H. Barnard, 1932:159, fig. 93.

Halirages stebbingi.—Alonso, 1980:10, fig. 7 (not Schellenberg, 1931).

Diagnosis.—Calceoli abundantly present; posterior pereonites not formed into posterolateral sharp wings in adults; outer rami or uropods 1–2 with several marginal spines in two rows; dorsal tooth of pleonite 3 usually as large as tooth on pleonite 2.

Material.—BMNH Holotype Hermit Island, Magellan Strait, Chile, Antarctic Expedition, female "a" 19.8 mm, lacking antenna 2 (illustrated). BMNH 1928.12.1: 2122–27, Syntype Falklands, R. Vallentin Expedition, formerly identified as *regis,* one specimen. BMNH 1936.11.2: 1381–84, st. 53, 12.5.1926, Discovery 0–2 m, female "b" 14.80 mm, identified as *huxleyanus* by K. H. Barnard. BMNH 1936.11.2: 1381–84 (Part), st. 56, 16.5.1926, Discovery BtS 10.5–16 m, identified as *huxleyanus* by K. H. Barnard, five specimens partly fragmented.

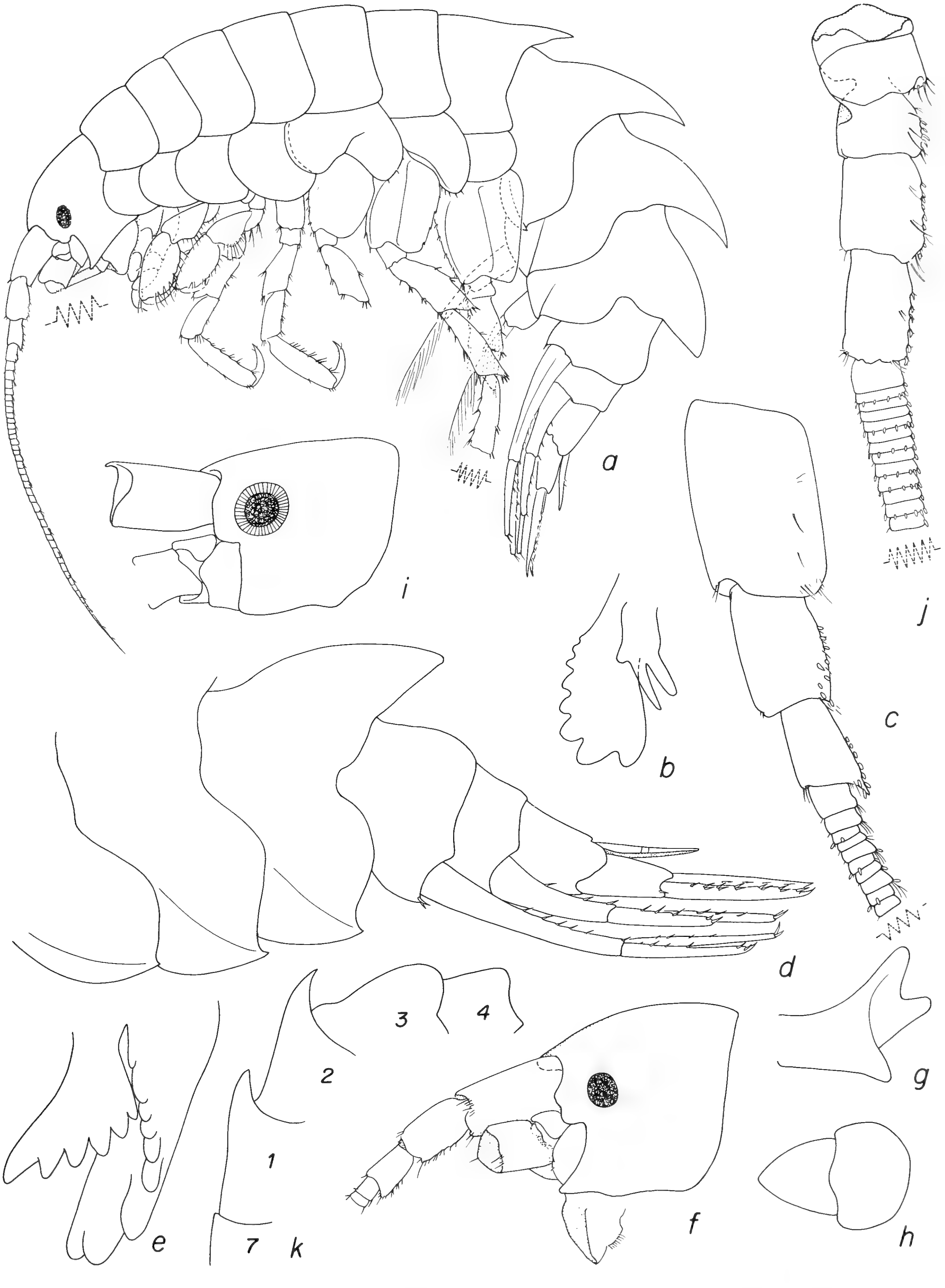

Fig. 2. *Austroregia huxleyana*: holotype, female "a" 19.8 mm, *a,* Body; *b,* Apex of right mandible; *c,* Antenna 1 lateral; *d,* Pleon; *e,* Apex of left mandible; *f,* Head; *g,* Right lacinia mobilis; *h,* Prebuccal, anterior view, dorsal to right. Female "b" 14.8 mm: *i,* Head; *j,* Antenna 2, medial; *k,* Pleonite 7 (left) to pleonite 4 (right).

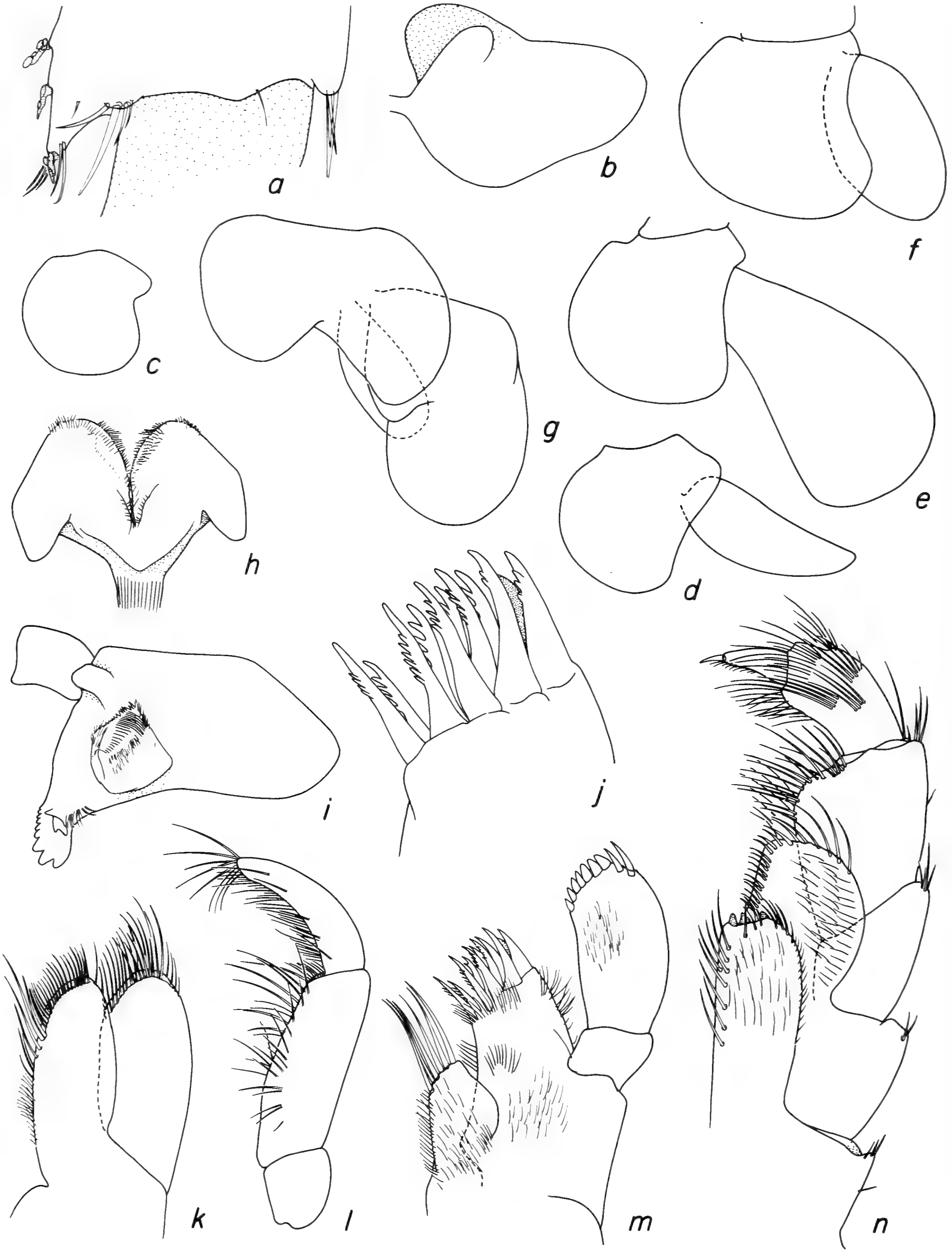

Fig. 3. *Austroregia huxleyana*: holotype, female "a" 19.8 mm, *a,* Region of accessory flagellum; *b,* Gill 6; *c,* Coxa 1; *d,* Coxa 2 and oostegite; *e,* Coxa 3 and gill; *f,* Coxa 4 and oostegite; *g,* Coxa 5 and oostegite (small) and gill (large); *h,* Lower lip; *i,* Right mandible; *j,* Outer plate of maxilla 1; *k,* Maxilla 2; *l,* Palp of right mandible; *m,* Maxilla 1; *n,* Maxilliped.

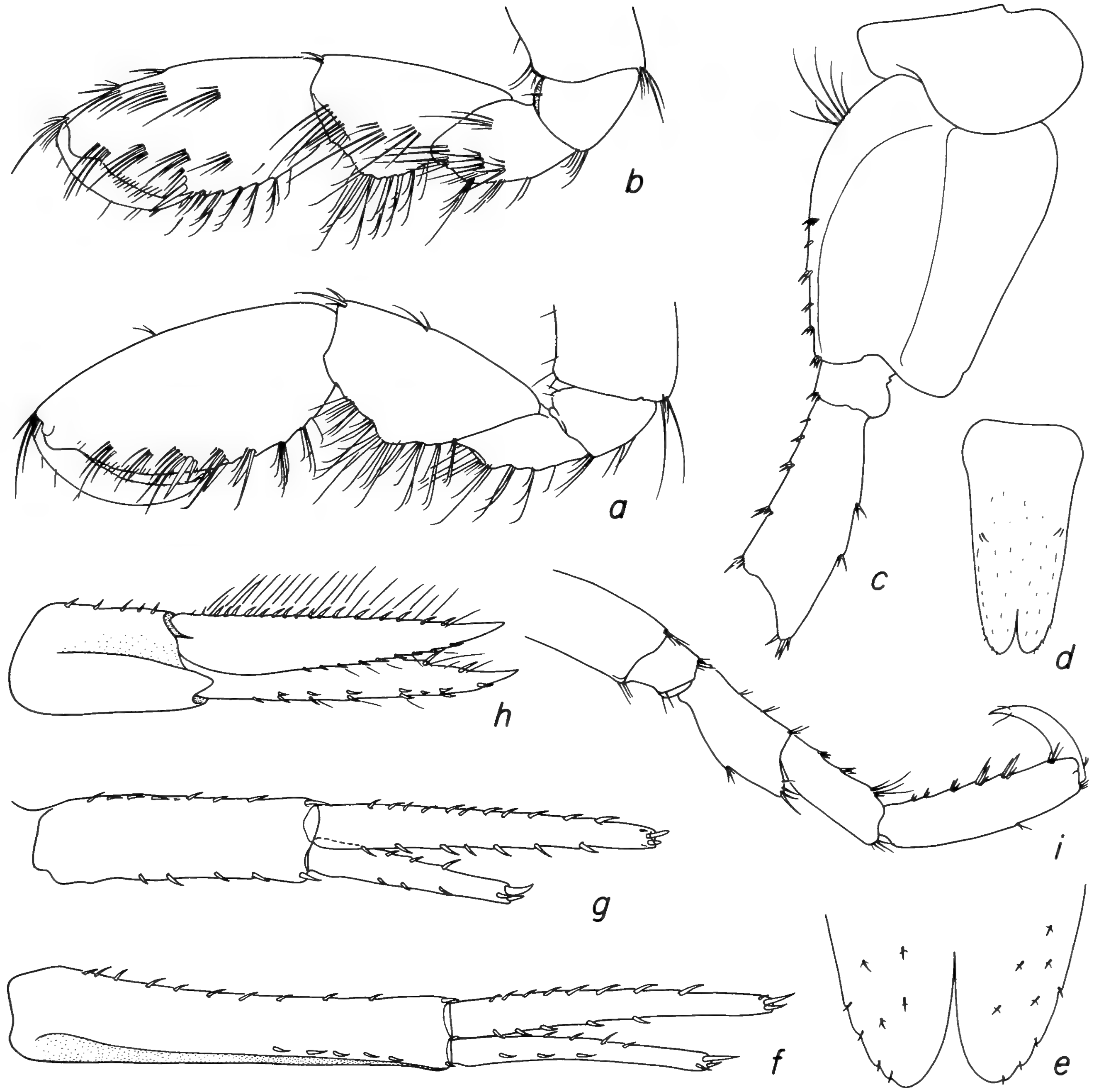

Fig. 4. *Austroregia huxleyana*: holotype, female "a" 19.8 mm, *a,* Gnathopod 1, lateral; *b,* Gnathopod 2, medial; *c,* Pereopod 7; *d, e,* Telson; *f–h,* Uropods 1, 2, 3; *i,* Pereopod 4.

Description of holotype female "a" 19.8 mm.—Antenna 2 missing, pereopods 5–7 broken, not available from better specimen, no enlarged views of pereopods 4–6 possible. Rostrum small, blunt; eyes small, circular, formed of ommatidia surrounding dark core of pigment, lateral cephalic lobes not protruding, truncate, antennal sinus weak, concave, bounded by tooth below. Antenna 1 about 50 percent as long as body, peduncle short, articles successively shorter, articles 2 and 3 with weak apicoventral tooth, each with 8+ ventral calceoli, accessory flagellum fused to peduncle, formed of small squared boss bearing one long and 3 short setae, primary flagellum with 44 articles, some basal articles of bead form, first slightly enlarged and subrectangular, others following of varying sizes in sets of 2 and 3, narrower to broader, calceoli present, terminal member of each set with groups of aesthetascs, broad articles with aesthetascs = 1,2,4,5,8,12,15,18,22,25,29,33,26, aesthetascs on these articles posterior, numbers

= 3,5+,2+,3+,5+,4+,3+,4+,4,4,3,2,2, for the most part calceoli occurring in complex positions similar to complex setal distributions of following species, *regis,* for example ("a" = anterior, "i" = inner, "o" = outer, "p" = posterior, from lateral views), article 1 with 0, article 2 = 1p, article 3 = 2a,1-0,1p, article 4 = 1p, article 5 = 1p, articles 6,9,13 = 2a,2-0,3i,1p, articles 7,8, 10,12,14,15,17,18,20,22,24,25,27,29,31,33, and 35–44 = 1p, articles 11,16,19,21,23,26, 28,30,34 = 1a,1-2-0,2-3i,1-2p, article 32 = 2a,2-0,1i,2p. Antenna 2 missing (see next specimen).

Body weakly depressed, pereonites shallow, lacking lateral ridges above coxae, not produced strongly posterolaterally, but weakly on 7, from dorsal view these segments not forming lateral wings, pereonite 7 with posterodorsal tooth, pleonites 1–2 with larger tooth, pleonite 3 with equally long thicker tooth, urosomites 1–3 rounded above. Coxae shorter than depth of pereonites, coxae 1–4 softly quadrate, with rounded distal corners, almost subcircular, coxae 3–4 weakly excavate behind, posterior lobe of coxa 5 as long as coxa 4, coxa 6 not shorter than 5, coxa 7 shortest, unlobed; coxae poorly armed.

Epistome and labrum rounded truncate anteriorly, see illustration for anterior view. Right and left incisors multitoothed, right lacinia mobilis with about 3 teeth, left with 6 teeth, about 8 right and 9 left rakers, each with extra interrakers, molar strongly triturative, palp article 2 densely setose medially, article 3 weakly bent, with no outer basal setae (=A-setae), inner margin with several C-setae and many D-setae, apex with 8+ E-setae. Lower lip lacking inner lobes. Inner plate of maxilla 1 subrectangular, with 6 apicomedial setae, outer plate with 11 mostly denticulate spines, palp article 2 symmetrical on both sides, with 7 thick apical spines, 2 thinner apicolateral spines, no facial subdistal setae. Inner plate of maxilla 2 as long as and scarcely narrower than outer plate, lacking facial row of setae, medial margin with three or four setae stouter and longer than apical cluster. Inner plate of maxilliped with 3 stout apical spines, one ventromedial coupling spine (not shown in illustration), outer plate broad and squat, with six apical setae, medially with thin tapering setae occasionally in pairs, palp articles 1–2 broad, 1–2 with few apicolateral and 2 with many medial setae, article 3 weakly geniculate, moderately setose medially, dorsolateral face with groups of setae, dactyl stubby, with short apical nail and many accessory inner setules.

Gnathopods small, first scarcely larger than second, wrists slender, barely lobate, hands much longer than wrists, ovatorectangular, palm of gnathopod 1 very oblique, defined by group of two facial spines, with two secondary groups outside dactylar apex on posterior margin of hand, dactyl simple, curved, lined with bent setules; palm of gnathopod 2 slightly better defined, relatively shorter than on gnathopod 1. Pereopods 3–4 as illustrated, locking spines 3 diverse members, posterior margins of article 6 with five armament sets each with two or three spines and spinules, dactyls simple, each with inner marginal and outer facial setule. Article 2 of pereopods 5–7 diverse, weakly ovate to more sharply trapezoidal successively, subrectangular distally, weak to strong posteroventral lobe present, limb lengths increasing successively. Gills present on coxae 2–6; oostegites poorly developed but of slightly expanded form on coxae 2–5, slightly pointed on coxa 2, paddle shaped on coxae 3–4, small and paddle shaped on coxa 5, setae absent but marked by humps or sockets.

Epimera 1–3 alike, each with convex posterior margin, sharp and weakly turned posteroventral tooth connected to lateral ridge, otherwise naked. Outer rami of uropods 1–2 shortened, all rami bearing apical spines and two marginal rows of spines, both upper margins of peduncle on uropods 1–2 with row of spines, those on uropod 1 lateral margin confined to distal half. Peduncle of uropod 3 slightly elongate, with five medial spines, rami extending equally, slightly curved apically, sharp, each with two rows of marginal spines, these spines doubled on outer margin of outer ramus, inner margin of inner ramus also strongly setose, other margins with sparse setae mostly apical. Telson elongate, basally broadened, weakly tapering, cleft about 20 percent of its length, each side of apex with four setules in tandem.

Female "b" 14.80 mm.—Enlargement of head illustrated; antenna 2 illustrated, articles 3–5 of peduncle furnished with ventral calceoli, articles 4–5 very short, flagellum thick, with 52 articles, last vestigial, aesthetascs absent, articles short and bead-like, calceoli present in relatively uniform pattern ("a" = anterior, "m" = medial, "p" = posterior), 1p present on articles 1,3,4,6,8, 11,13,16,19,23,25,29,31,34,36,39,41,43,45, 48, none present on articles 50–51, articles 9,10,12,14,15,17,18,20,24,26,30,32, with 2a,3m,2p, articles 2,5 with 2a,4m,2p, article 7 with 2a,3m,1p, articles 21,22,27,28,33,37 with 2a,2m,2p, article 35 with 2a,2m,3p, articles 38,40,42,44,46 with 2a,1m,3p, article 47 with 2a,3p, article 49 with 2a,2p.

Dorsal body cuspidation of 2-toothed form, only pleonites 1–2 each with medium sized dorsoposterior tooth; pereopods 5–7 and uropods 1–3 badly broken.

Distribution.—Boreal South America and Falkland Islands, 0–55 m.

Austroregia regis (Stebbing)
Figs. 5–7

Halirages huxleyanus.—Stebbing, 1888: 902, pl. 73 (not Bate, 1862).

Bovallia regis Stebbing, 1914:362, pl. 8.

Halirages regis.—K. H. Barnard, 1932:161, fig. 94.

Halirages stebbingi Schellenberg, 1931:176, pl. 1, fig. 1.

Diagnosis.—Calceoli usually absent; posterior pereonites formed into posterolateral sharp wings in adults; outer rami of uropods 1–2 with two or fewer marginal spines; dorsal tooth of pleonite 3 usually smaller than tooth of pleonite 2.

Material.—Syntypes, BMNH 1928.12.1: 2122–27, Roy Cove, Falkland Islands, low spring tide, R. Vallentin Expedition: Lectotype, here selected, male "c" 6.81 mm (illustrated); syntype male "d" 6.28 mm; syntype juvenile "e" 5.75 mm and one other juvenile. Following specimens all misidentified formerly as *H. huxleyanus*: BMNH 1928.12.11: 2019–26 (part), Stanley Harbour, Falkland Islands, coll. Stebbing, three giant specimens, male "f" 19.80 mm (illustrated body), female "g" 23.81 mm (illustrated head and coxae 1–4), female "h," unmeasured. BMNH 1928.12.1: 2019–26 (part), Rock pools, Falkland Islands, 20.11.1910, R. Vallentin Expedition, coll. Stebbing, three specimens, one large, one medium, one small. BMNH 1928.12.1: 2019–26 (part), Falkland Islands, 20.vi.1910, coll. Stebbing, nine juveniles. BMNH 1936.11.2: 1381–84 (part), st. 55, 16.v.1926. BtS 10–16 m, Discovery det. K. H. Barnard, one small form. BMNH 1936.11.2: 1385, st. 56, 16.v.1926, Net: BtS, 10.5–16 m, "white, very heavily mottled with deep crimson," Discovery det. K. H. Barnard, female "i," unmeasured, with long head tooth.

Description of lectotype male "c" 6.81 mm.—Antenna 2 missing, pereopods 3–4, 6–7 broken, pereopods 5–7 illustrated from better specimen, left mandible only described, no enlarged views of head, epistome, labium, pereopods 3–7, dactyls. Rostrum small, blunt; eyes circular, with dark core of pigment, lateral cephalic lobes not protruding, truncate, antennal sinus weak, straight, oblique. Antenna 1 almost 55 percent as long as body, peduncle short, articles successively shorter, accessory flagellum fused to peduncle, formed of small squared boss bearing 1 long and 3 short setae, primary flagellum with 30 articles, some basal articles of bead form, first slightly enlarged and rectangular, others following of

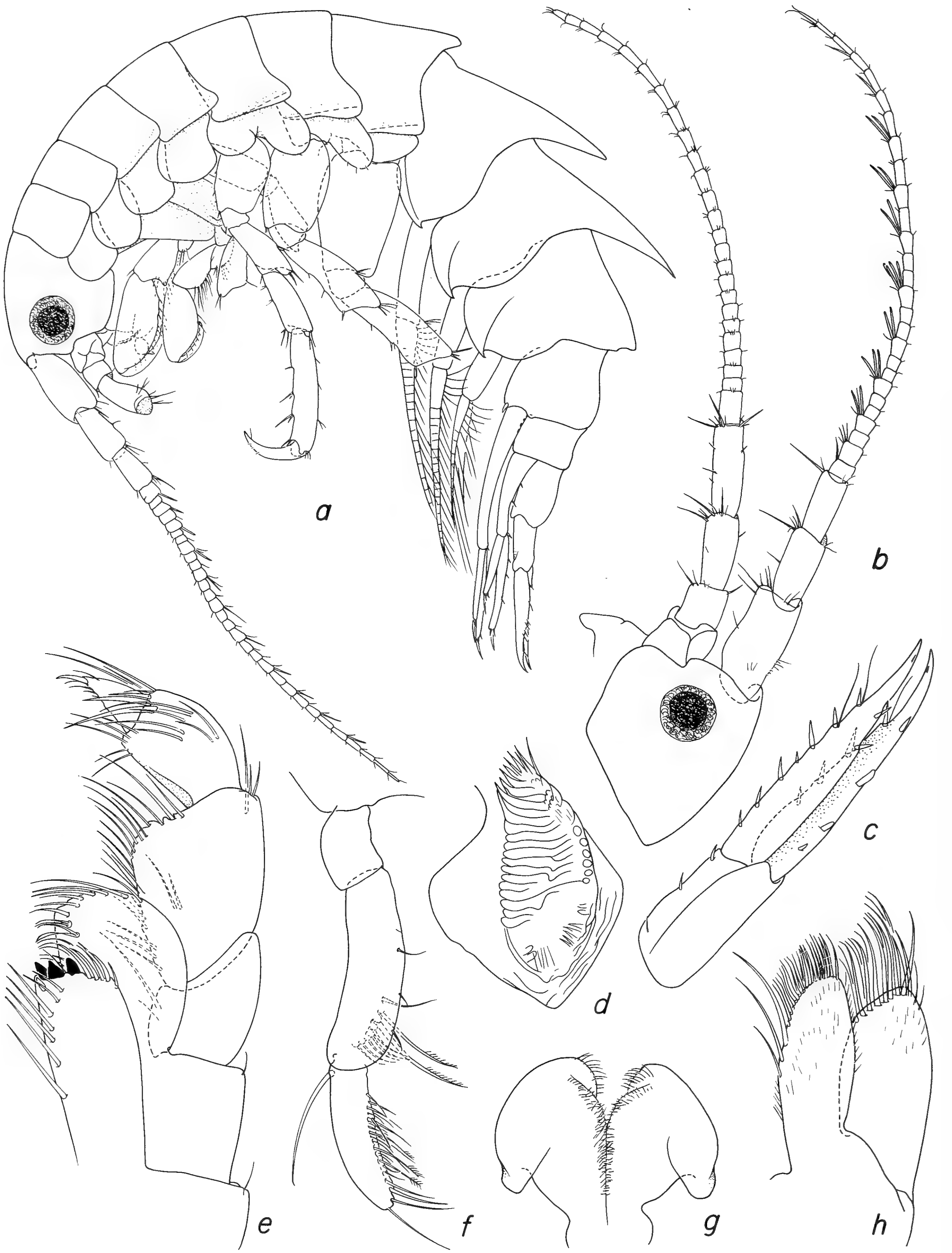

Fig. 5. *Austroregia regis*: lectotype male "c" 6.81 mm, *a,* Body; *c,* Left uropod 3; *d,* Right molar; *e,* Maxilliped; *g,* Lower lip; *h,* Maxilla 2. Male "d" 6.28 mm, *b,* Head. Male "c" 6.81 mm, *f,* Right mandibular palp.

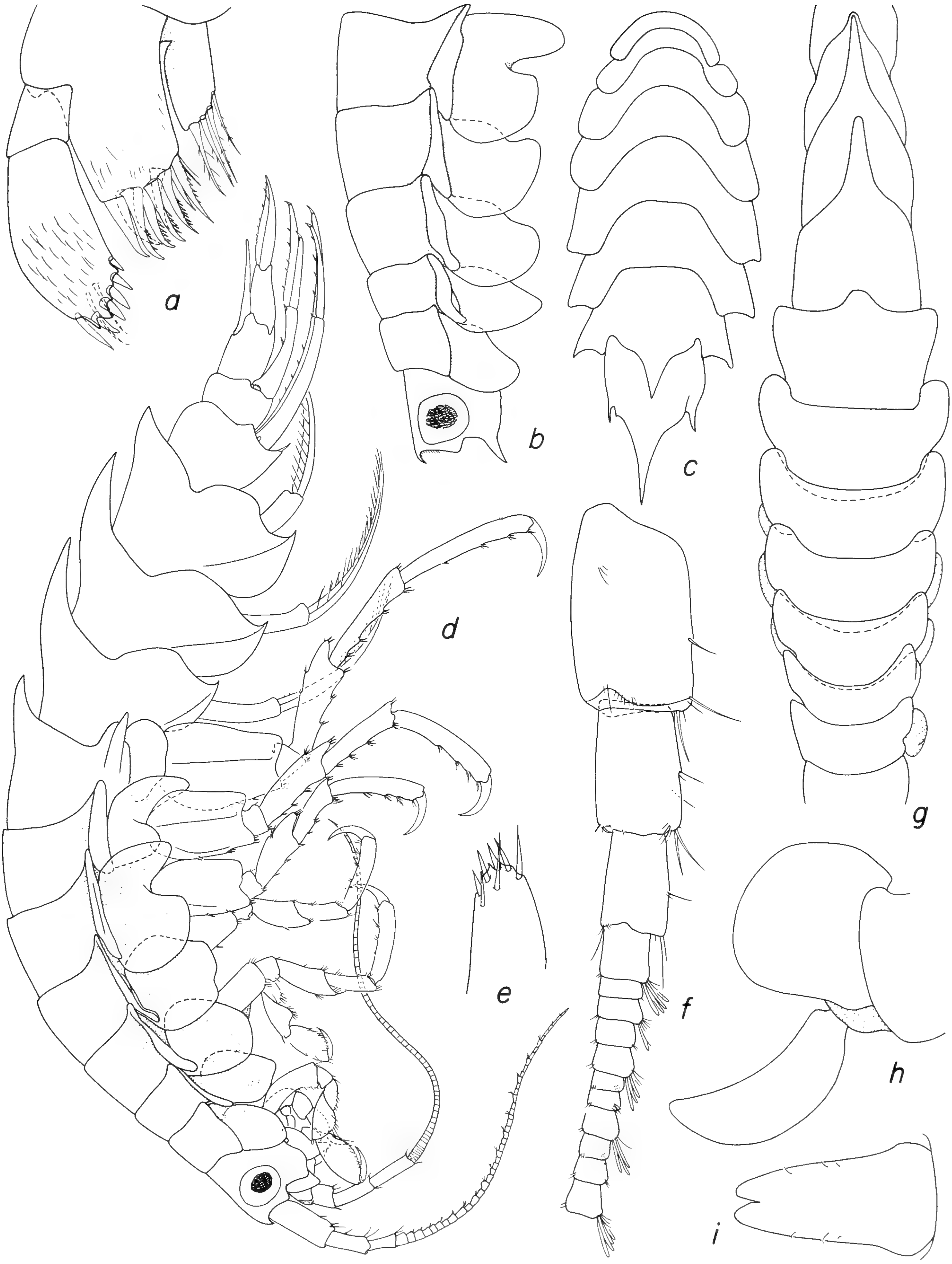

Fig. 6. *Austroregia regis*: lectotype male "c" 6.81 mm, *a,* Maxilla 1; *e,* Other palp of opposite maxilla 1; *f,* Medial antenna 1; *g,* Dorsal body, head at bottom; *h,* Coxa 4 with gill; *i,* Telson. Female "g" 23.81 mm, *b,* Head and pereonites 1–5. Male "f" 19.8 mm, *c,* Dorsal body from pereonite 1 (top) to pleonite 1 (bottom); *d,* Body.

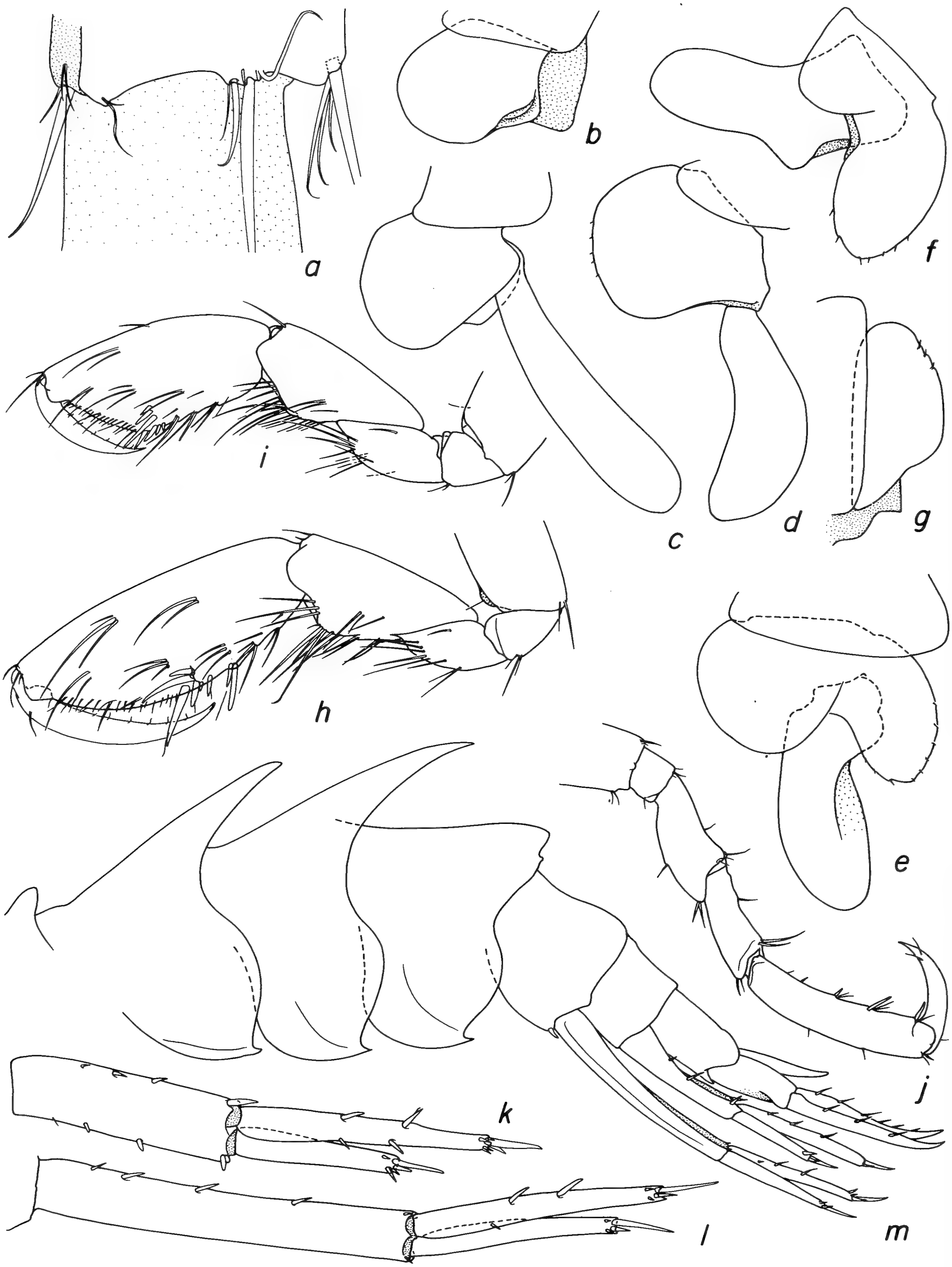

Fig. 7. *Austroregia regis*: lectotype male "c" 6.81 mm, *a,* Region of accessory flagellum; *b,* Coxa 1; *c,* Coxa 2 with gill; *d,* Coxa 3 with gill; *e,* Coxa 5 with gill; *f,* Coxa 6 with gill; *g,* Coxa 7; *h,* Gnathopod 1, medial; *i,* Gnathopod 2, medial; *k, l,* Uropods 2 and 1; m, Pleon. Male "d" 6.28 mm, *j,* Pereopod 3.

varying sizes in sets of 2 and 3, narrower to broader, calceoli absent, terminal member of each set with groups of aesthetascs, broad articles with aesthetascs = 1,3,5,8,11,14,17, 20,22,24,26,28, aesthetascs on these articles posterior, numbers = 4,2,2+,3+,4,3,3,1,2, 2,1,1, setal distributions complex, for example ("a" = anterior, "i" = inner, "m" = marginal, "s" = submarginal, from lateral views), article 1 with 2a,2p, article 2 = 0a,1p, article 3 = 2a,5p, article 4 = 3m,2p, article 5 = 2a,4+p, articles 6,9,12,15 = 2–3s,3i, articles 7,10,13,16 = 2–3m,3–4p, articles 8,11,14,17 = 2–3a,3–5p, etc. Antenna 2 missing (see next specimen).

Body weakly depressed, pereonites shallow, pereonites 3–7 with weak lateral ridge above coxae, pereonites 4–7 produced posterolaterally, weakly on 7, from dorsal view these segments forming lateral wings more rudimentarily expressed on pereonites 1–3, pereonite 7 with posterodorsal tooth, pleonites 1–2 with larger tooth, pleonite 3 with short weakly acute dorsal projection, urosomites 1–3 rounded above. Coxae shorter than depth of pereonites, coxae 1–4 softly quadrate, with rounded distal corners, coxae 3–4 weakly excavate behind, posterior lobe of coxa 5 as long as coxa 4, coxa 6 scarcely shorter than 5, coxa 7 shortest, unlobed; coxae poorly armed.

Epistome and labrum as shown for *A. huxleyanus.* Incisors and laciniae mobiles of mandibles heavily encrusted, similar to *A. huxleyanus,* thus right incisor with about eight teeth, right lacinia mobilis with three teeth, about six rakers, molar strongly triturative, palp article 2 with most setae forming apicolateral row, article 3 weakly bent, with one (right) or two (left) outer basal setae (=A-setae), inner margin with several C-setae and many D-setae, apex with two E-setae. Lower lip lacking inner lobes. Inner plate of maxilla 1 subrectangular, with four apicomedial setae, outer plate with nine mostly denticulate spines, palp article 2 asymmetrical on both sides, with five thick apical spines, one thinner apicolateral spine, two facial subdistal setae on left side, right side with five thin apical spines and two subapical setae. Inner plate of maxilla 2 slightly longer and narrower than outer plate, lacking facial row of setae, medial margin with three setae stouter and longer than apical cluster. Inner plate of maxilliped with three stout apical spines, one ventromedial coupling spine, outer plate broad and squat, with six apical setae, medially with thin blades occasionally in pairs, palp articles 1–2 broad, 2 with few apicolateral and many medial setae, article 3 weakly geniculate, poorly setose medially, dorsolateral face with groups of setae, dactyl stubby, with short apical nail and three accessory inner setules.

Gnathopods small, first larger than second, wrists slender, barely lobate, hands much longer than wrists, subrectangular, palm of gnathopod 1 very oblique, defined by group of three or four marginal and two facial spines, with secondary group outside dactylar apex on posterior margin of hand, dactyl simple, curved, lined with bent setules; palm of gnathopod 2 better defined, relatively shorter than on gnathopod 1. Pereopods 3–4 as illustrated for specimen "d" below, locking spines 2 diverse members, posterior margins of article 6 with three or four armament sets each with one spine and from zero to two short setae, dactyls simple, each with inner marginal and outer facial setule. Article 2 of pereopods 5–7 narrow, subrectangular distally, weak posteroventral lobe present, limb lengths increasing successively. Gills present on coxae 2–6.

Epimera 1–3 alike, each with convex posterior margin, sharp and strongly turned posteroventral tooth connected to lateral ridge, otherwise naked. Outer rami of uropods 1–2 shortened, each bearing only apical spines, inner rami with two rows of marginal spines besides apical cluster, peduncle of uropod 1 with only one small apicolateral spine, medial margin with five spines, peduncle of uropod 2 with three dorsolateral spines and one basal setule, medial margin with five spines. Peduncle of uropod 3 slightly elongate, with two medial spines and one basal seta, rami extending equally, curved apically, sharp, each with two rows of marginal spines, inner also with seta in last two apical spine sets, outer also with seta in last spine set medially, each ramus with subapical setule. Telson elongate, basally broadened, weakly tapering, cleft about 10 percent of its length, each side with three setules in tandem.

Male "d" 6.28 mm.—Pereopod 3 enlarged to show details.

Male "f" 19.80 mm.—Supposed terminal adult form, body illustrated: pereonites more alate posterolaterally, pereonites 2–7 with shelf above coxae, pointed on pereonite 7; coxae more diverse, coxa 2 bluntly pointed below, coxae 3–4 relatively larger than in juvenile form; antenna 2 as illustrated, articles 4–5 of equal length, flagellum "proliferate," basal article with new articles forming inside; dorsal tooth of pereonite 3 enlarged; apices of pereopods 6–7 illustrated on body.

Female "g" 23.81 mm.—Head with large anteroventral tooth below antennal sinus (illustrated). Coxae 3–4 sinuous posteroventrally. Outer ramus of uropod 2 with two marginal spines.

Female "h" large, unmeasured.—Outer ramus of uropod 1 with one marginal spine, of uropod 2 with one or two marginal spines (right and left); coxae acuminate as in female "g" but head lacking tooth.

Female "i" unmeasured.—Like female "g" but smaller, coxae more strongly acuminate; each outer ramus of uropods 1–2 with one marginal spine.

Discussion.—The lectotype is unfortunately a small male less than one-third as long as the largest adults known (as measured by parabolic method). It clearly has the flared-out posterolateral margins of the pereonites but not to the exaggerated degree of larger specimens. In large specimens the pereonal margins flare out laterally until they form horizontally projecting teeth. In some specimens the posterior margins of the flared teeth are incised posteriorly and have very extended lateral wings which look like separate processes from lateral view but which are simply more knife-like. Large adults occur in two forms: (1) head with large posteroventral tooth coupled with strongly acuminate anterior coxae and (2) head without strong posteroventral tooth coupled with poorly acuminate anterior coxae. Small specimens lack dorsally marginal spines on the outer rami of uropods 1–2 whereas larger adults have as many as three and two spines on the outer rami of uropods 1 and 2 respectively. No calceoli have been discovered in our specimens of this species, although Stebbing shows calceoli in his original description.

Relationship.—Differing from *A. huxleyanus* in the presence of flared margins on the pereonites, the poorly spinose outer rami of uropods 1–2 and the usual absence of calceoli. The specimen figured by Stebbing (1888: pl. 73) has calceoli. The condition of coxae in adult *huxleyana* resembles that of juvenile *regis* so that coxal forms are not necessarily definitive in comparing the two species.

There remains the question of whether *A. regis* is congeneric with *A. huxleyana* because the two species differ in the setal formulas on article 3 of the mandibular palp, in the spine numbers on the outer plate of maxilla 1, the difference in setal presence on the palps of maxilla 1, and the symmetricity of those palps. Article 3 of the mandibular palp lacks A-setae in *huxleyanus*; the latter has 11 spines on the outer plate of maxilla 1 whereas *A. regis* has 9; and the palps are symmetrical and lack subdistal setae in *A. huxleyana.* There also remains the problem of speciation in this group and because of the extensive demal variations already noted, very large and widespread collections of antarctic materials should be assembled to study the life history and variations in the group.

Distribution.—Tierra del Fuego and Falkland Islands, 0–55 m.

Acknowledgments

Dr. Roger J. Lincoln of the British Museum of Natural History made extensive contributions to this work and kindly supplied the SEM photographs. I thank Linda B. Lutz of Vicksburg, Mississippi, for inking our illustrations and Patricia B. Crowe and Kimberly R. Cleary of the Smithsonian Institution for their assistance in the laboratory.

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TWO NEW SPECIES OF WOOD-BORING *LIMNORIA* (CRUSTACEA: ISOPODA) FROM NEW ZEALAND, *L. HICKSI* AND *L. RENICULUS*

Marilyn Schotte

Abstract.—*Limnoria hicksi* is described and distinguished from *L. indica* Becker & Kampf, 1958 by the structures on the fifth pleonite and the pleotelson. *Limnoria reniculus,* similar to *Limnoria foveolata* Menzies, 1957, *L. saseboensis* Menzies, 1957, *L. sexcarinata* Kühne, 1975 and *Limnoria sublittorale* Menzies, 1957, differs from all four in the structure of the fifth pleonite, pleotelson and morphology of the lacinioid seta of the right mandible.

At present only two reliably identified wood-boring isopods of the genus *Limnoria* have been reported from New Zealand. These are *L. quadripunctata* Holthuis from Portobello (Hurley 1961), Auckland Harbour (McQuire 1964), and Port Nicholson (Ralph & Hurley 1952), and *L. tripunctata* Menzies, also from Auckland Harbour (McQuire 1964). Menzies (1959) listed *L. quadripunctata* site records for isopods he examined from Auckland, Wellington, and Napier, previously thought to be specimens of *L. lignorum* (Rathke). Chilton (1914) had assigned the latter name to wood-borers found in timbers in Auckland and Lyttleton harbors and in piles from Akaroa Harbour. The latter isopod, whose name was assigned to most limnoriids before Menzies' 1957 monograph, has an Arctic-boreal distribution and has been reliably reported only in the Northern Hemisphere from 39° to 58°N and from Iceland (Menzies 1957). Two alga-borers have been found in New Zealand, *Phycolimnoria stephenseni* Menzies, in floating *Lessonia* near Auckland Island (also Macquarie Island), and *P. segnis* (Chilton) from seaweed in Lyttleton and Akaroa harbors (Menzies 1957) as well as from Portobello (Hurley 1961).

Across the Tasman Sea, *Limnoria quadripunctata* has been found recently in Australia at Goat Island and Sydney Harbour in association with *L. indica* and *L. tripunctata* Menzies, as well as in Tasmania (Cookson 1987). Hale (1929) reported *L. lignorum* from Port Lincoln but this identification is undoubtedly erroneous. *L. sublittorale* Menzies has been collected from New South Wales (Menzies 1957), as has *Phycolimnoria rugosissima* Menzies. An additional alga-borer, *P. nonsegnis* Menzies from Tasmania, brings to eight the total number of limnoriids thus far known from the Australia-New Zealand region.

Material of the new species has been deposited at the National Museum of New Zealand in Wellington and the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Family Limnoriidae

Limnoria (*Limnoria*) *hicksi,* new species

Figs. 1A–D, 2A–F, 3A–E

Material.—Holotype, NMNZ Cr. 5702, ♀ tl 4.0 mm, Paratype, USNM 205960, ♀ tl 3.3 mm (on slide and SEM stub), stn K6 R/V *Kalinovo,* 177°39′05″E, 37°23′07″S to 177°36′06″E, 37°23′07″S, off New Zealand, 1075–1100 m, in rotting wood, 23 Nov 1981, coll. G. R. F. Hicks.

Description.—Female: Pigment absent. Pleonite 5 with a row of four proximal tubercles and two somewhat larger distal tu-

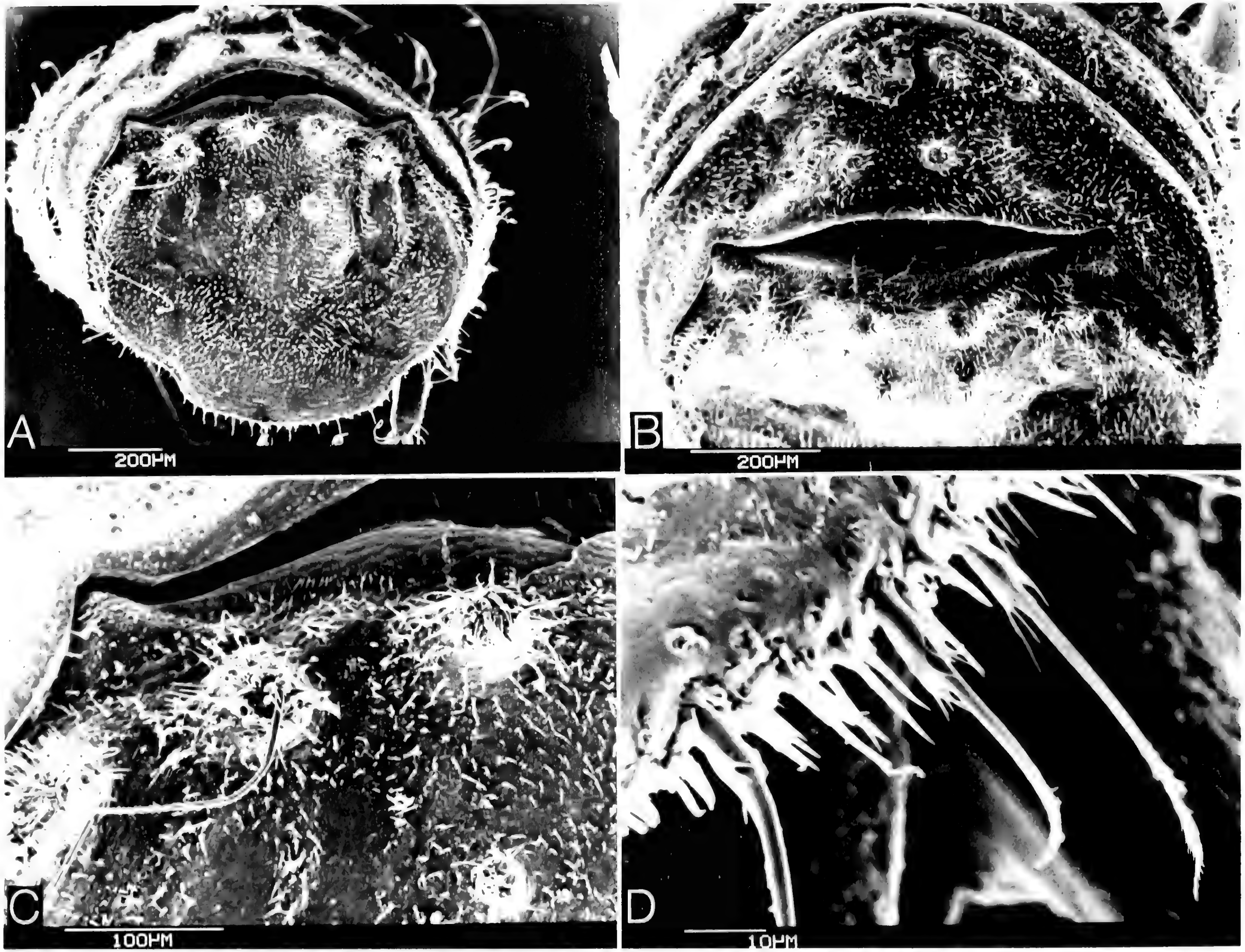

Fig. 1. *Limnoria hicksi*: A, Pleotelson; B, Fifth pleonite and anterior pleotelson; C, Tubercles at base of pleotelson enlarged; D, Spination on distal margin of pleotelson.

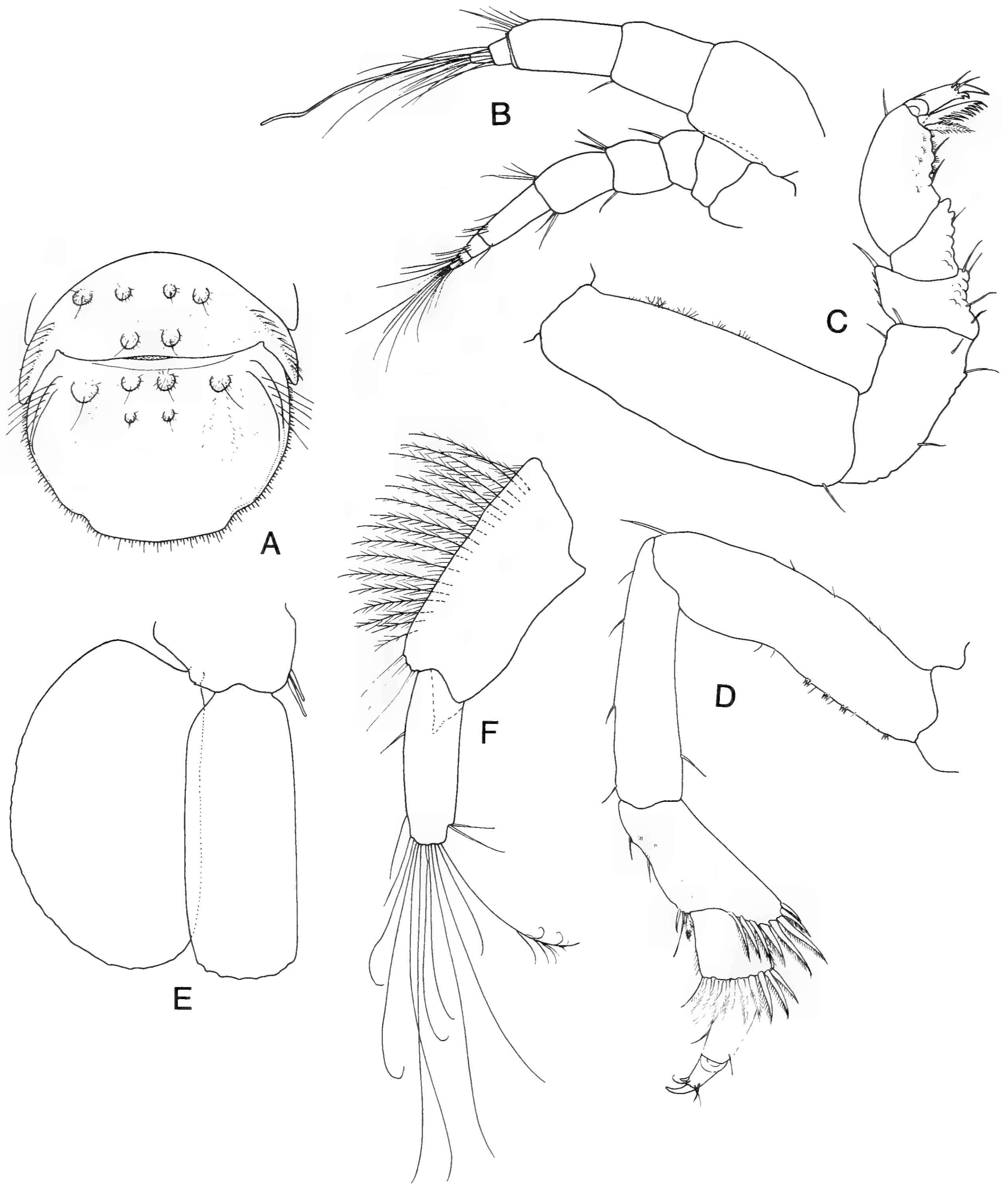

Fig. 2. *Limnoria hicksi*: A, Fifth pleonite and pleotelson; B, Antennule and antenna; C, First pereopod; D, Seventh pereopod; E, First pleopod of female; F, Uropod.

bercles, all bearing short spinules. Lateral crests of pleonite 5 with long setae. Pleotelsonic margin not evenly rounded but with pair of shallow symmetrical notches in posterior third. Base of pleotelson with a row of four large tubercles and pair of smaller tubercles posterior to these, all spinose (Fig. 1C) and bearing at least one long seta. Lateral crests with long setae. Surface of pleotelson regularly spinulose except for bare patches lateral to posterior tubercles. Posterior margin not tuberculate but with both simple and sheathed spines (Fig. 1D).

Antennular peduncle of three articles, first

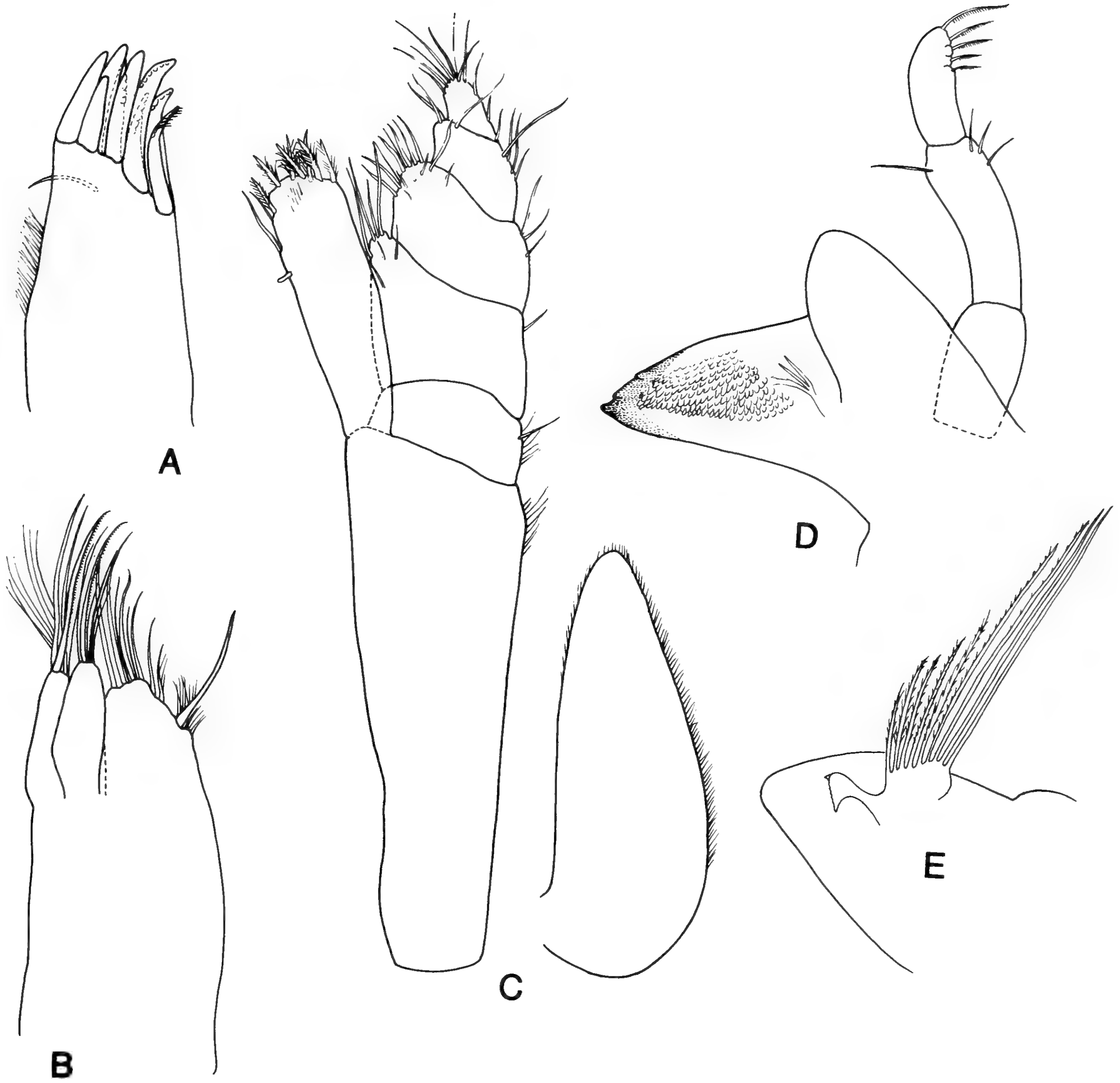

Fig. 3. *Limnoria hicksi*: A, Outer lobe of first maxilla; B, Second maxilla; C, Maxilliped; D, Left mandible; E, Lacinioid seta of right mandible.

and third articles subequal in length; flagellum consisting of one very short basal article and two subequal articles. Antennal flagellum of four articles, first article longer than three distal articles combined.

Mandibular palp of three articles, second article longest, terminal article bearing five distal fringed spines; "rasp" of left incisor strongly sclerotized; spine row of right mandible of nine laciniate spines, distal edge of lacinioid seta broad, very finely toothed and acute at ends. Maxilla 1 with nine stout setae, four of which provided with blunt teeth and one with setules. Maxilla 2 as figured. Maxillipedal endite with single coupling hook and six setose spines on distal margin; articles 2 and 3 of palp subequal in length; epipod about three times longer than greatest width, not reaching distal margin of basipod.

Pereopod 1 with bidentate accessory spine at base of dactylar unguis; propodus with one dentate and one fringed posterodistal spine. Pereopod 7, accessory spine of dactyl small and apparently not bidentate; carpus with many fringed spines on distal margin; merus with anterodistal margin somewhat produced and bearing numerous fringed

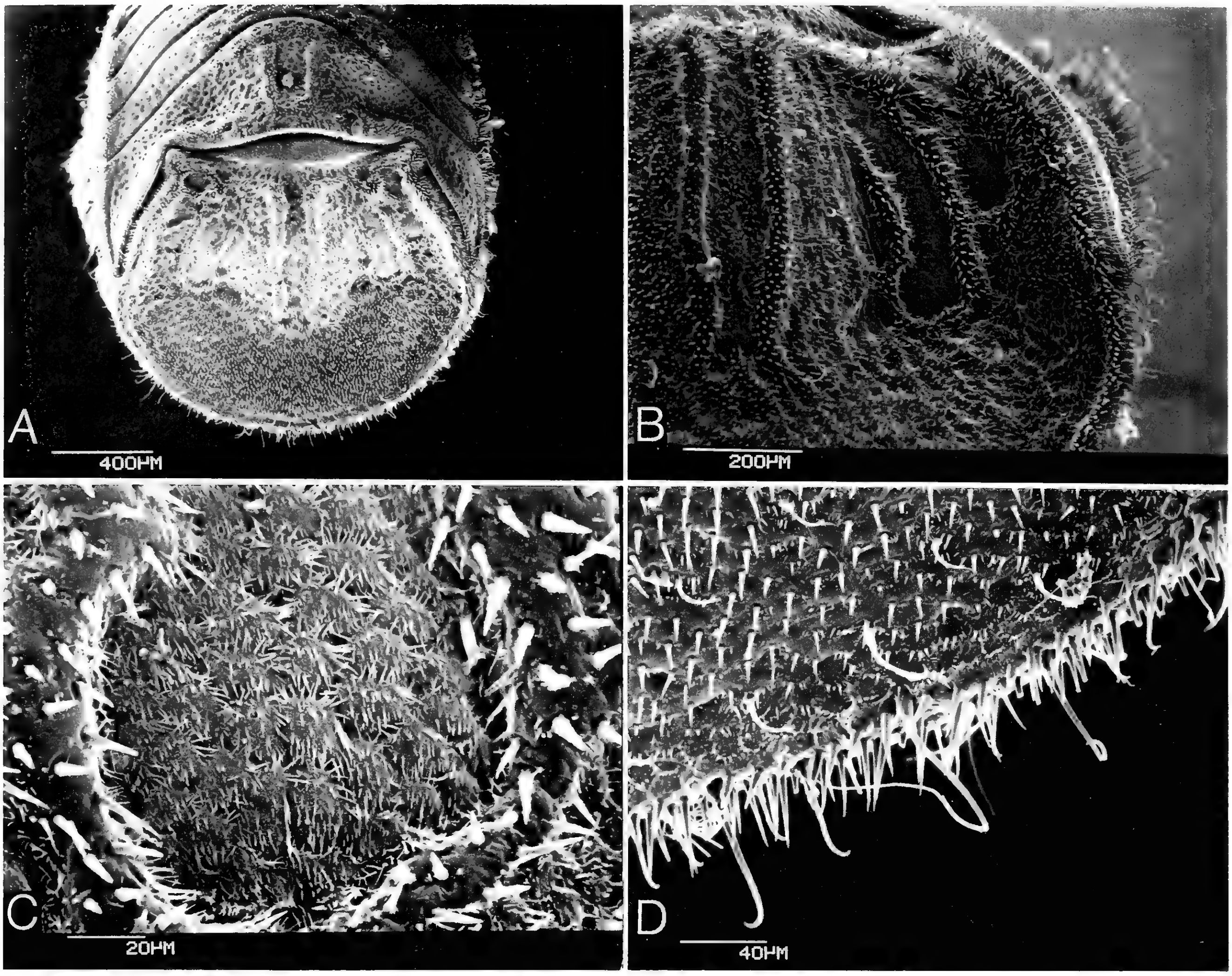

Fig. 4. *Limnoria reniculus*: A, Pleotelson and fifth pleonite; B, Pleotelsonic surface enlarged; C, Interior surface of kidney-shaped carina enlarged; D, Pleotelsonic margin.

spines visible in lateral view. Endopods of pleopods 1 and 2 of female distally truncate. Structure of male second pleopod unknown. Uropodal exopod less than one-half length of endopod; latter bearing one plumose seta and several terminal setae of varying lengths; peduncle with row of short, simple setae on outer margin and additional row of long plumose setae near margin.

Remarks.—The male of the sexually dimorphic *L. indica* is the only other known limnoriid with six basal tubercles on the pleotelson arranged similarly to those in *L. hicksi.* Instead of additional tubercles on the fifth pleonite, *L. indica* in both sexes possesses two subparallel longitudinal carinae bearing setae, thereby distinguishing it from *L. hicksi.*

Etymology.—The new species is named for its collector, Dr. Geoffrey R. F. Hicks, National Museum of New Zealand, Wellington, New Zealand.

Limnoria (*Limnoria*) *reniculus,* new species

Figs. 4A–D, 5, 6A–G, 7A–E

Material.—Holotype, NMNZ Cr. 5703, ovig. ♀, tl 5.0 mm, Allotype, NMNZ Cr. 5704, ♂, 4.4 mm, Paratypes, NMNZ Cr. 5705, 11 ovig. ♀, 16 ♀, 15 ♂, South Taramaki Bight, North Island, New Zealand, R/V *James Cook,* sta J20/25/84, 40°56.4′S, 174°44.0′E to 40°59.8′S, 174°43.7′E, in rotting wood, 144–182 m, 29 Nov 1984, coll. G. R. F. Hicks. Paratypes, USNM 205961, 11 ovig. ♀, 15 ♀, 14 ♂, from same locality. Other material: USNM 205962, 1 specimen, South Taranaki Bight, New Zealand,

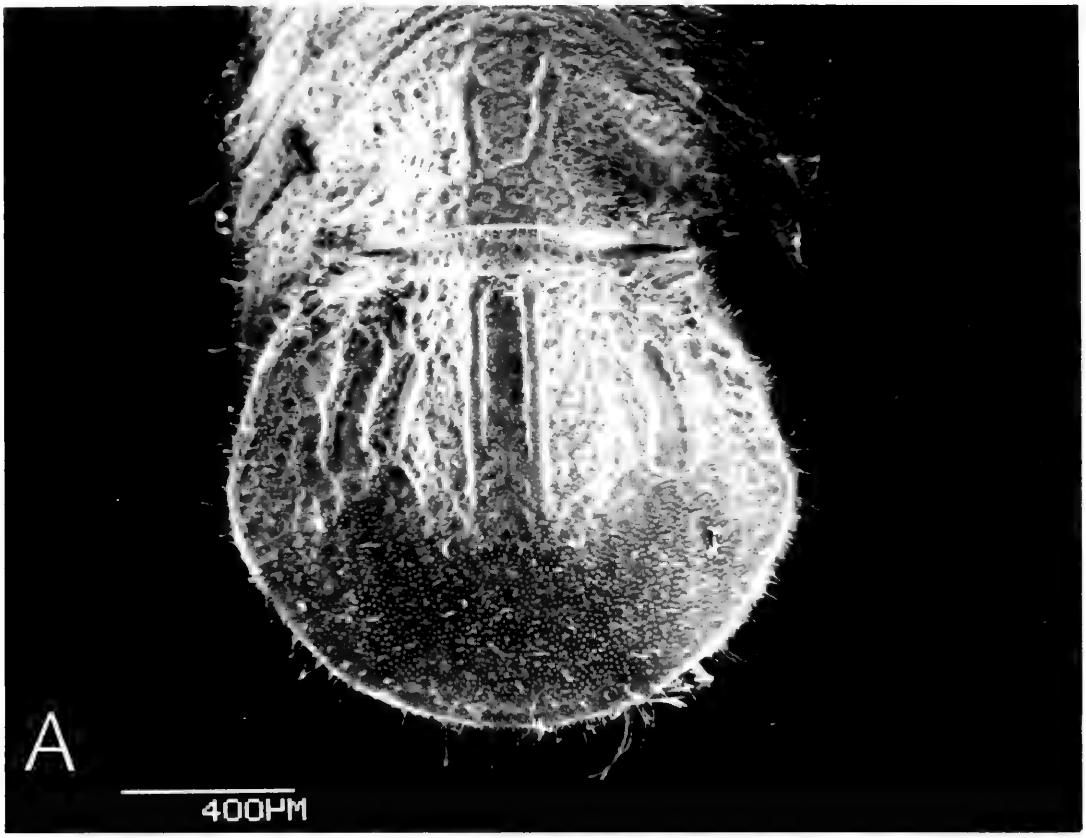

Fig. 5. *Limnoria reniculus*: Different specimen from same lot as specimen in Fig. 4, pleotelson and fifth pleonite.

sta J20/16/84, 40°33.0'S, 173°04.6'E to 40°31.7'S, 173°01.2'E, in rotting wood, 47–52 m, 28 Nov 1984, coll. G. R. F. Hicks.—USNM 205963, 5 specimens, sta J15/40/84, 40°33.4'S, 173°04.6'E to 40°32.4'S, 173°02.6'E, in rotting wood, 44–52 m, 28 Nov 1984, coll. G. R. F. Hicks.—USNM 205964, 11 specimens, sta J16/6/84, 37°51'S, 177°19'E to 37°51'S, 177°15'E, in rotting wood, 48–49 m, 17 Sep 1984, coll. G. R. F. Hicks—USNM 205965, J15/22/84, 41 specimens, 42°21.6'S, 170°49.5'E to 42°24.4'S, 170°48.1'E, in rotting wood, 179–184 m, 3 Sep 1984, coll. G. R. F. Hicks.—USNM 205966, sta J15/40/84, 5 specimens, 42°59.4'S, 170°16.5'E to 42°57.2'S, 170°19.3'E, in rotting wood, 60–62 m, 5 Sep 1984, coll. G. R. F. Hicks.—USNM 205967, 6 specimens, sta J15/28/84, 42°45.8'S, 170°28.2'E, in rotting wood, 50–64 m, 4 Sep 1984, coll. G. R. F. Hicks.—USNM 205968, 3 specimens, sta J20/12/84, 40°46.7'S, 173°48.0'E to 40°47.9'S, 173°47.3'E, in rotting wood, 60–65 m, 27 Nov 1984, coll. G. R. F. Hicks.—USNM 205969, 6 specimens, off North Island, New Zealand, R/V *James Cook*, sta J9/70/84, 38°02'S, 174°37'E to 38°06'S, 174°36'E, in rotting wood, 50–51 m, 3 Jun 1984, coll. G. R. F. Hicks.—USNM 205970, 3 specimens, sta J16/2/84, 37°39'S, 177°28'E to 37°39'S, 177°24'E, in rotting wood, 134–137 m, 17 Sep 1984, coll. G. R. F. Hicks.—USNM 205971, 8 specimens, New Zealand, off Cape Runaway, *Wanaka*, sta WK 3/19/85, 37°29.9'S, 177°47'E, in Log A, 450–481 m, 8 Dec 1985.—USNM 205972, 19 specimens, New Zealand, Bay of Plenty, east of Alderman Island, NMNZ Cr. 5152, from timber, 400–520 m, Jun 1969, coll. R. D. Cooper.—USNM 205973, 14 specimens, New Zealand, WNW White Island, Tumokemoke Knoll, R/V *Tangaroa* (NZOI sta R 76), 37°29.1'S, 176°54.7'E, in twig, 248–283 m, 20 Jan 1979.

Description.—Male: Dorsal integument of pereon and pleon rather foveolate, especially pleonite 5. Pleonite 5 with somewhat variable U-shaped carina (Figs. 4A and

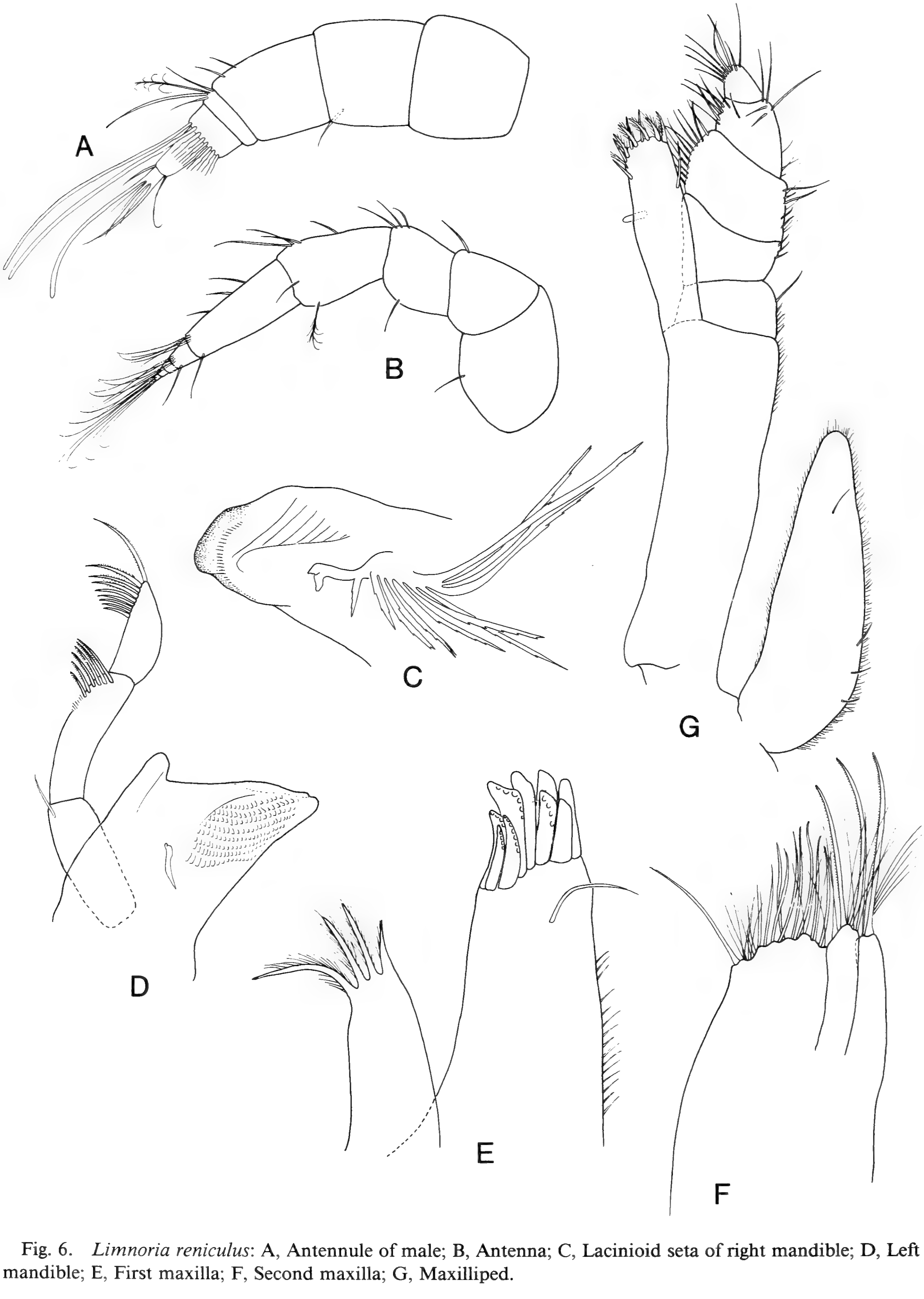

Fig. 6. *Limnoria reniculus*: A, Antennule of male; B, Antenna; C, Lacinioid seta of right mandible; D, Left mandible; E, First maxilla; F, Second maxilla; G, Maxilliped.

5). Pleotelson densely spinulose with two rounded submedian ridges basally, flanked on either side by irregular, kidney-shaped carinae, apparently bare interiorly but actually covered with tiny spinules (Fig. 4C). Submedian ridges becoming obsolete distally. Margins of pleotelson not tuberculate, having multiple rows of simple, unsheathed spines. Female dorsum as in male.

Antennular peduncle of three articles; flagellum of male consisting of basal article, much shorter than wide, penultimate article with many aesthetascs ringing distal margin, and terminal article half as wide as preceding article. Antennal flagellum of 4 articles, basal article longer than 3 distal articles together. Mandibular palp of 3 articles, two proximal articles subequal in length; article 2 with 6 distal fringed spines; terminal article bearing 9 distal fringed spines; spine row of left mandible a single process; spine row of right mandible of 10 laciniate spines, increasing in length proximally; lacinioid seta with two lobes, one elongate and blunt, the other short and jagged; incisor with strongly sclerotized cusp. Maxilla 1 and 2 as figured. Maxillipedal endite with single coupling hook, eight spines on distal margin, five of which setulose; palpal article 3 longest and widest; epipod more than three times longer than greatest width, distally rounded and not reaching base of palp. Pereopod 1, bidentate accessory spine at base of dactylar unguis; propodus with 1 dentate, plus one fringed posterodistal spine. Carpus and merus with short rows of rounded scales on posterior surface. Pereopod 7, accessory spine of dactyl barely bidentate; carpus with many fringed spines on distal margin; merus produced anterodistally, bearing many fringed spines encircling distal margin. Appendix masculina of pleopod 2 of male articulating proximal to midlength on median margin of endopod, extending beyond ramus. Uropodal endopod elongate, about four times longer than wide and bearing five plumose setae and several lateral and terminal simple setae; uropodal exopod a slightly curved claw; peduncle with row of setae inserted medially to lateral margin.

Remarks.—*L. reniculus* may be confused with *L. saseboensis* Menzies, which also has submedian longitudinal ridges on the pleotelson, especially if debris obscures the kidney-shaped carinae in uncleaned specimens of the former. The U-shaped carina on pleonite 5 in *reniculus* may vary but the subparallel ridges do not join proximally as they appear to do in *saseboensis.* Menzies' description notes the posterior edge of the pleotelson and lateral crests as tuberculate with "spike-like bristles on the margin." SEM photos (Fig. 4) do not reveal obvious tubercles in the present species. The two species also differ somewhat in the shape of the lacinioid seta of the right mandible with "two medially curved teeth at apex" in *L. saseboensis. L. sublittorale* Menzies from Australia also has a pair of longitudinal carinae on the telson but apparently lacks other surface ornamentation there. The lacinioid seta of the right mandible has two recurved teeth instead of a blunt lobe as in *L. reniculus. L. foveolata* Menzies, while also foveolate on the pleotelson and pleonite 5, has carinae on both segments which are more irregular than those in the new species, and it lacks the kidney-shaped features. The lacinioid seta of *L. foveolata* as figured by Menzies has three teeth at the apex.

The new species also resembles *L. sexcarinata* Kühne. Examination of type material of the latter species reveals the carina of pleonite 5 as "horseshoe-shaped" and the curving ridges on the pleotelson do not join distally. Kühne's (1975) description states that the lacinioid seta of the right mandible, apparently a good character for distinguishing members of this genus, is "branched and furnished at the end with teeth." SEM photos of *L. sexcarinata* show the presence of tubercles and sheathed spines on the pleotelsonic margin, neither of which exist in *L. reniculus.*

Etymology.—The Latin *reniculus* (little

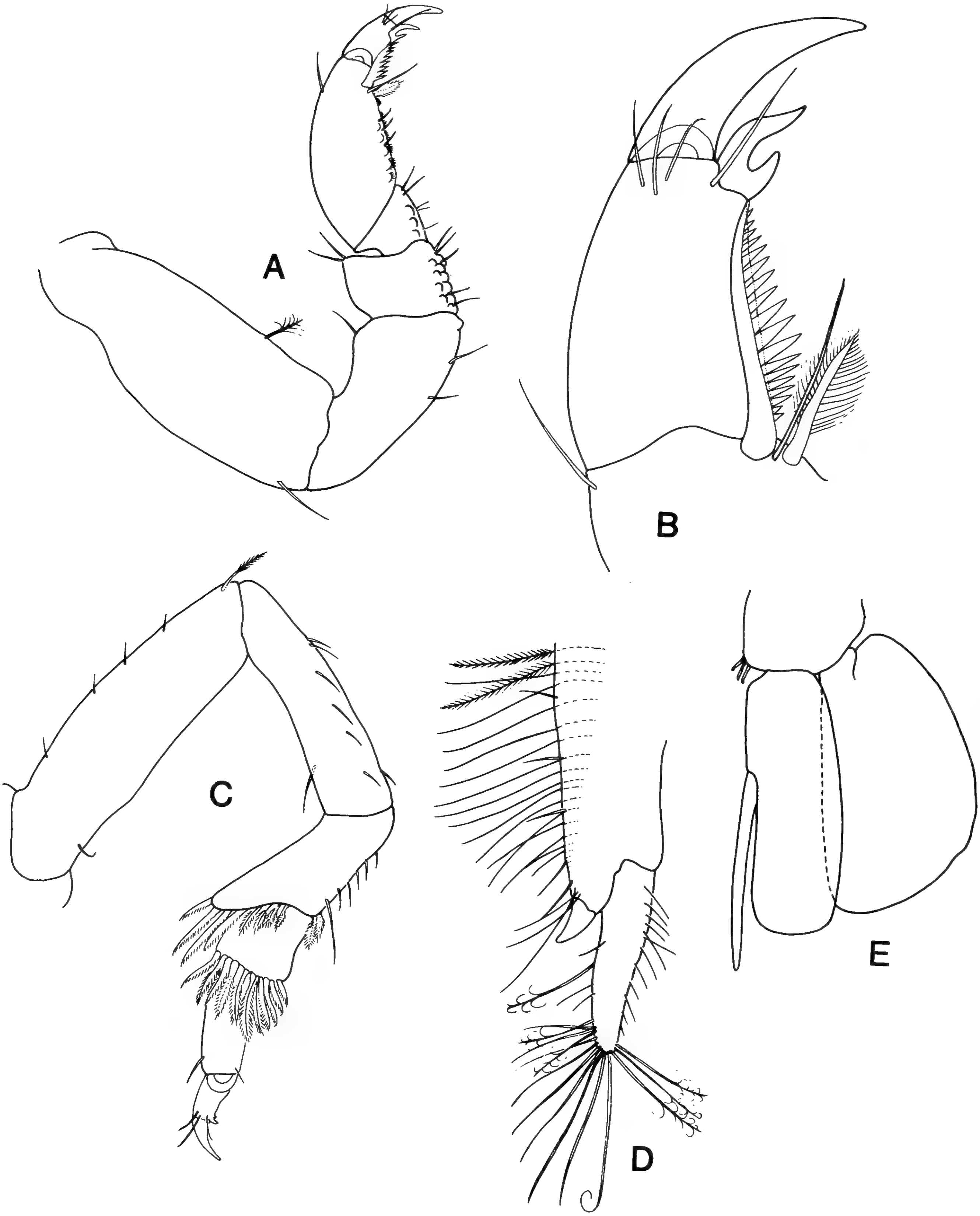

Fig. 7. *Limnoria reniculus*: A, First pereopod; B, Dactyl of first pereopod enlarged; C, Seventh pereopod; D, Uropod; E, Second pleopod of male.

kidney), proposed as a noun in apposition, refers to the shape of the outline of the carinae flanking middorsal ridges on the pleotelson.

Acknowledgments

Material described in this paper was kindly provided by Dr. Goeffrey R. F. Hicks of the National Museum of New Zealand. Mrs. Susann Braden of the NMNH assisted with preparation of the scanning electron micrographs. The manuscript benefitted from comments by Laurie Cookson and Brian Kensley, both of whom reviewed the manuscript.

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SOME ASPECTS OF THE BIOLOGY OF *RHOPALOPHTHALMUS TATTERSALLAE* PILLAI, 1961 (CRUSTACEA, MYSIDACEA) AND EXTENSION OF RANGE INTO THE KHOR AL SABIYA, KUWAIT (ARABIAN GULF)

Stephen A. Grabe

Abstract.—*Rhopalophthalmus tattersallae* Pillai was collected from the Khor al Sabiya, Kuwait, extending its known range from the Indian Ocean to the northern Arabian Gulf. Population density was greatest in early fall when juveniles predominated and was lowest in mid-winter. Spawning activity was greatest in April, May, July, and August, and lowest in mid-winter. Brood size was correlated with body size; largest females and broods occurred January through May and smallest females and broods occurred July through November. Sex ratio was close to 1:1 on most dates. A small number of *R. tattersallae* were parasitized by an unidentified dajid isopod.

Rhopalopthalmus tattersallae was described by Pillai (1961; cited in Pillai 1965) from specimens collected in coastal waters off Kerala State, India. To my knowledge, there have been no subsequent records of its occurrence. Fifteen species of *Rhopalophthalmus* have been described (Mauchline 1980) and all are inhabitants of neritic or estuarine waters (Tattersall 1957; Hodge 1963; Pillai 1965, 1973; Mauchline & Murano 1977; Wooldridge & Erasmus 1980). This paper presents some basic life history information for *R. tattersallae* and records its range extension into the northern Arabian Gulf.

Methods.—Daytime zooplankton collections were taken at stations in Kuwait Bay and the Khor al Sabiya (Fig. 1) from September 1981 through September 1982. Duplicate step-oblique tows were made with a 0.5 m diameter plankton net outfitted with 0.202 mm and 0.505 mm mesh. The sampling schedule is summarized in Table 1. Sample volumes were measured with a digital flow meter. Additional samples were collected at Station 614 on 27 May and 21 September 1982 specifically for mysids. A 0.505 mm mesh net was towed near-bottom (horizontally); sample volumes were not recorded.

All mysids were sorted from each sample, identified to life stage, and carapace length (CL) measured (tip of the rostrum to the posterior border of the carapace).

Brood sizes (number of larvae) were determined only for those females whose marsupia appeared undisturbed. The presence of an unidentified ectoparasitic isopod (Dajidae) was recorded.

Monthly population density in the Khor al Sabiya (Stations 614 & 615) was based upon the September and October 1981 0.202 mm collections and the November through August 0.505 mm mesh collections. To facilitate interpretation of seasonal changes in population structure and breeding, samples were pooled for each date at the Khor al Sabiya stations. Assumptions were made, then, that the populations at the two stations in the Khor were structurally similar and that the 0.202 and 0.505 mm mesh nets were similarly efficient in sampling all life stages of this species.

In studies of mysid populations in which

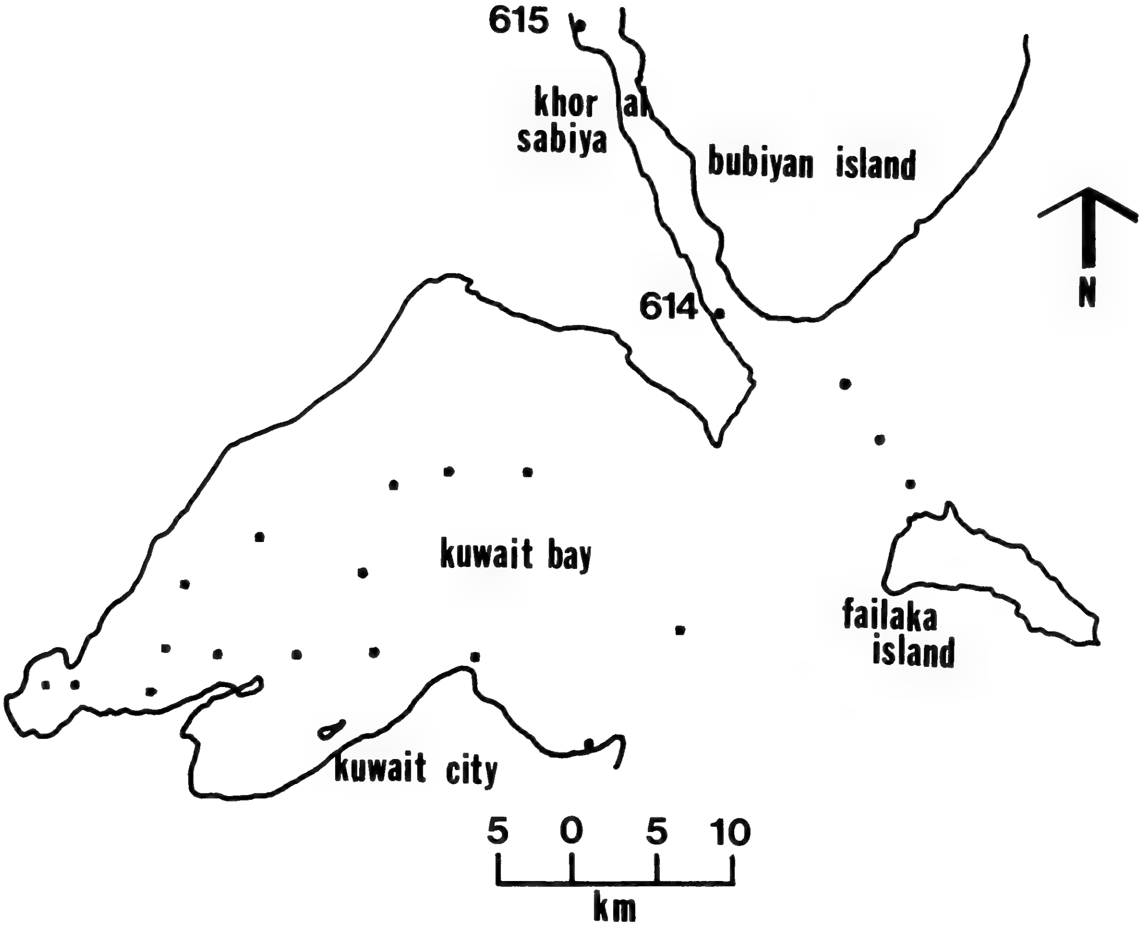


Fig. 1. Location of the sampling stations in Kuwait Bay and Stations 614 & 615 in the Khor al Sabiya used to survey the *Rhopalophthalmus tattersallae* population during 1981–1982.

longitudinal differences in population structure have been observed, there have either been marked differences in habitat (e.g., depth) within the water body (Mauchline 1970) or there was evidence for recruitment, transport and maturation of a coastally spawned population (Hulburt 1957). Since the Khor al Sabiya stations were of similar depth, temperature, salinity and dissolved oxygen (Dames & Moore 1983) and since there was no evidence of recruitment from Kuwait Bay (see below), the first assumption seems tenable.

The second assumption, that of comparable sampling abilities of the two gears, is more questionable. Sampling rates of the two gears were generally similar in the Khor al Sabiya (12.6 vs. 12.7 m^3/minute for the 0.202 and 0.505 mesh, respectively; Dames & Moore 1983). A limited comparison of sampling efficiencies for Penaeidae mysis and postlarval stages found that abundance estimates of the two gears were comparable: 0.202 mm abundance $= -1.38 + 1.1$ (0.505 mm abundance); $r_{10} = 0.986$; $P < 0.01$ (Dames & Moore, unpublished data).

ANOVA (Sokal and Rohlf 1981) was used to test for differences in mean CL of mature females by sampling date, and regression analysis was used to evaluate the relationship between brood size and CL.

Results and discussion.—The Khor al Sabiya is a river-like channel separating the Sabiya peninsula on the northeastern shore of Kuwait Bay from Kuwait's Bubiyan Island (Fig. 1). Maximum depth is about 18 m but study areas averaged <10 m. Bottom sediments at Station 614 were generally rock-mud and shell debris and at Station 615, muddy sand and shell debris. Extremes in water temperature occurred during February (12.1°C surface, 11.8°C bottom) and

Table 1.—Sampling schedule for *Rhopalophthalmus tattersallae* in the Khor al Sabiya, Kuwait, September 1981 to September 1982.

	Mesh size			Mesh size	
Date	0.202 mm	0.505 mm	Date	0.202 mm	0.505 mm
17 Sep 81	X		26 Apr	X[a]	
27 Sep	X		12 May	X	X
14 Oct	X		18 May	X[a]	
28 Oct	X		27 May		X[b]
10 Nov		X	7 Jun	X	X
17 Nov		X	5 Jul	X[a]	
16 Dec		X	27 Jul	X	X
11 Jan 82		X	9 Aug	X[a]	
20 Feb		X	18 Aug	X	X
3 Mar	X	X	29 Aug	X[a]	
11 Apr	X	X	21 Sep		X[b]

[a] Station 614 only.

[b] Non-quantitative, near-bottom samples.

June (29.9°, 27.9°). Extremes in salinity occurred during April (32.6‰, 32.7‰) and June (40.4, 40.5‰) (Dames & Moore 1983).

Rhopalophthalmus tattersallae was collected throughout the year in the Khor al Sabiya but occurred in only 26% of the samples from Kuwait Bay. Highest densities occurred during autumn. Thereafter density declined through February before it increased again from April through August (Fig. 2). Concentrations of mysids were higher at Station 614 near the mouth of the Khor al Sabiya than at Station 615.

The relationship between Cl and TL was significant and highly correlated ($r_{63} = 0.99$). The regression equation is: $TL_{mm} = 3.88\ CL_{mm} - 0.41$.

Spawning activity was probably greatest during April, May, July and August when large (≥2.5 mm CL) sexually mature mysids and 0.7–0.8 mm CL juveniles composed respectively from 33 to 72% and from 3 to 13% of the population. Recruitment of juveniles from April through October (they composed from 32 to 82% of the population at this time) coincided with the peak in population density (Fig. 2). The presence of small, but sexually identifiable, mysids indicated that the summer-fall generation ma-

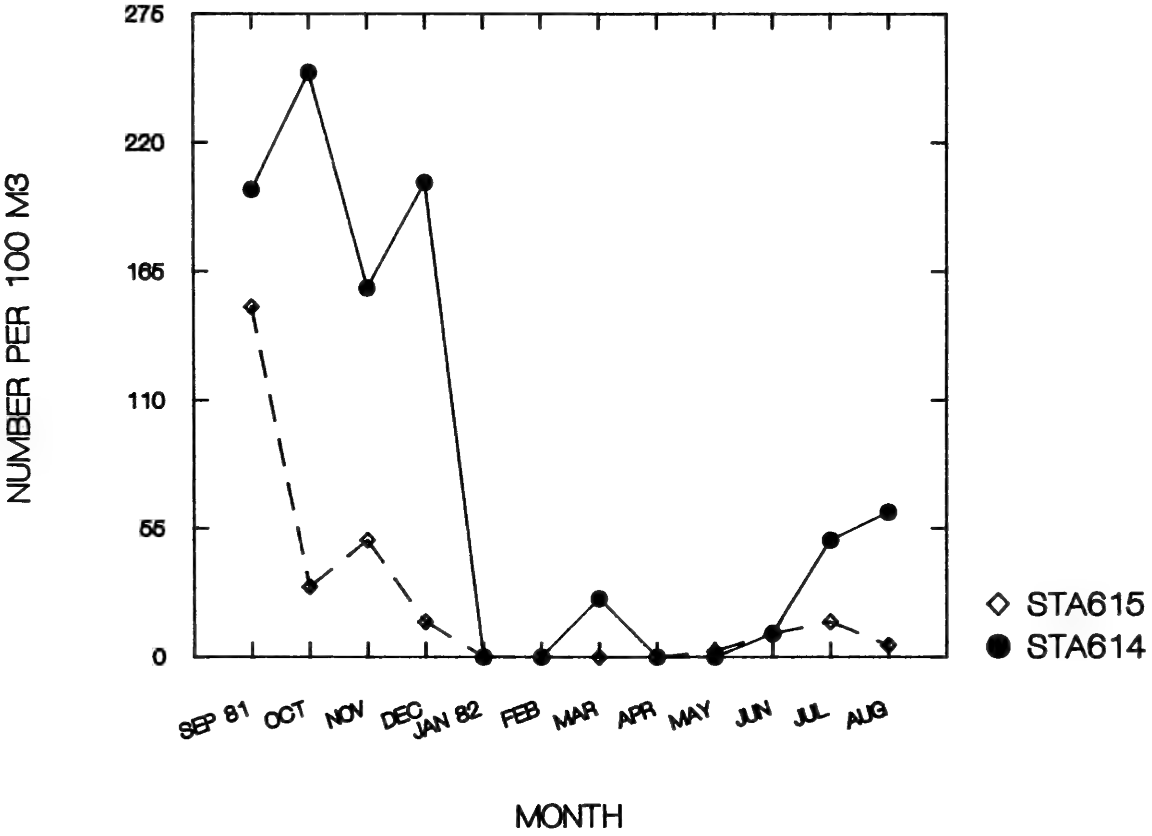


Fig. 2. Abundance (numbers/100 m³) of *Rhopalophthalmus tattersallae* in the Khor al Sabiya, Kuwait, September 1981–August 1982.

tured from September through November. These composed from 9 to 24% of the population. A relatively sparse overwintering population was characterized by large (≥2.5 mm CL) mature mysids and few juveniles. Brooding females were collected on 19 of the 22 sampling dates (Table 2) and brooding activity appeared to be greatest during May and from late July through August. The lowest incidence of brooding females occurred between mid-fall and mid-spring.

Brooding females ranged in size from 1.8 to 3.3 mm CL (Fig. 3) and ANOVA showed that there were significant differences between dates for mean CL of mature females ($F_{17,279} = 17.0$; $P < 0.001$). Brood size ranged from 2 to 23 larvae (Fig. 4) and the equation, Number of Larvae = $9.3\ CL_{mm} - 13.7$, was significant ($F_{1,121} = 64.0$; $P < 0.001$).

Table 2.—Percent of larvigerous *Rhopalophthalmus tattersalae* in the Khor al Sabiya, Kuwait, September 1981 to September 1982. Numbers in parentheses are numbers of specimens collected.[a]

Date	% Larvigerous	Date	% Larvigerous
17 Sep 81	25.0 (64)	12 May	80.0 (10)
27 Sep	0.0 (9)	18 May	100.0 (15)
14 Oct	16.7 (18)	27 May	14.3 (7)
28 Oct	6.3 (16)	7 Jun	50.0 (2)
10 Nov	3.6 (28)	5 Jul	0.0 (20)
17 Nov	2.4 (84)	27 Jul	75.0 (72)
16 Dec	0.7 (148)	9 Aug	66.7 (3)
11 Jan 82	7.7 (39)	18 Aug	64.0 (25)
3 Mar	33.3 (15)	21 Sep	25.0 (52)
11 Apr	66.7 (3)		

[a] Females were not collected on 20 Feb, 26 Apr and 29 Aug.

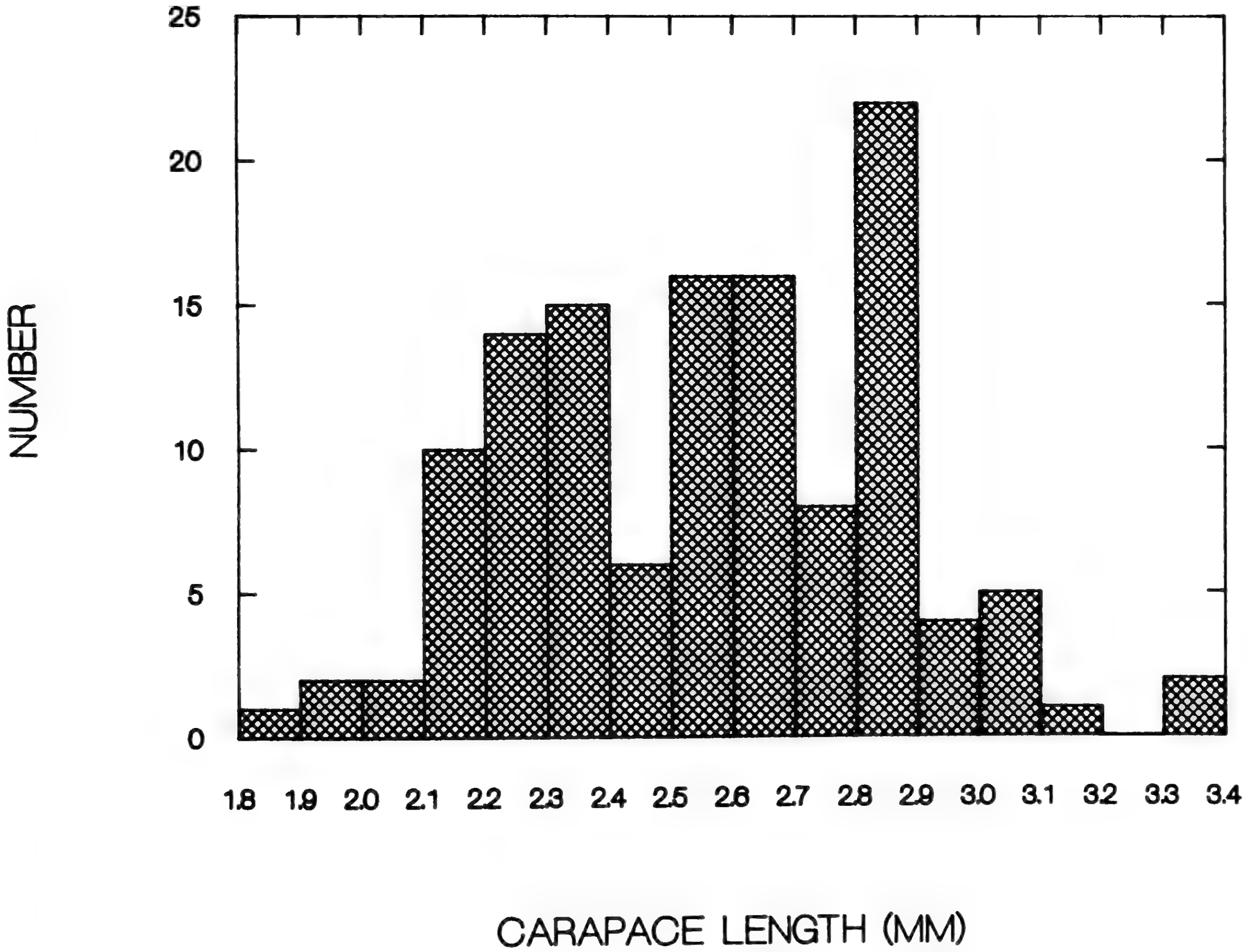


Fig. 3. Size frequency distribution of larvigerous *Rhopalophthalmus tattersallae* in the Khor al Sabiya, Kuwait, September 1981–1982.

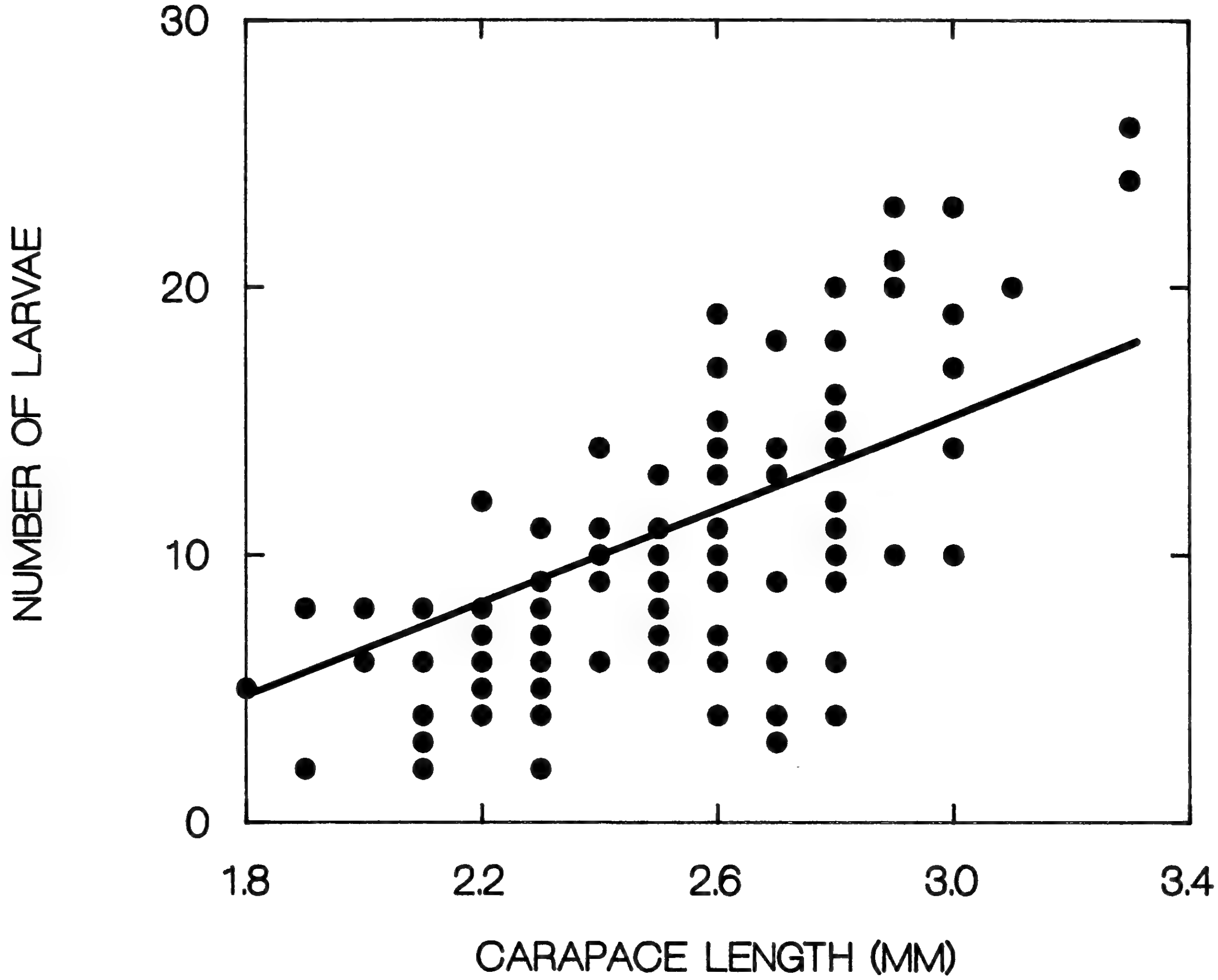
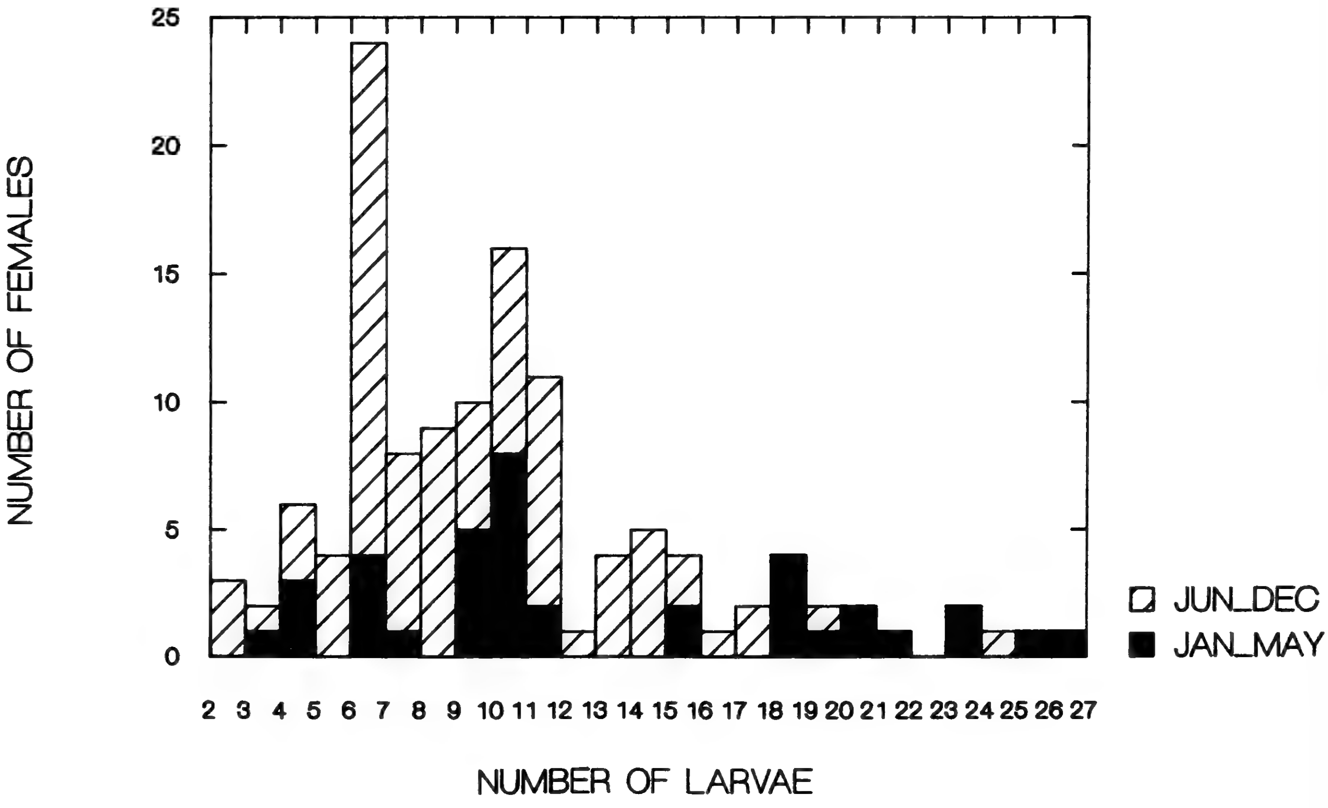


Fig. 4. Relationship between number of larvae and carapace length for *Rhopalophthalmus tattersallae* in the Khor al Sabiya, Kuwait, September 1981–1982.



Brood sizes were generally <10 larvae/female with only 6.6% carrying 20 or more larvae. Larger females and broods occurred from January through May and the smaller females and broods from July through September (Fig. 5). This is consistent with observations of other species of subtropical mysids which produce several generations per year (Mauchline 1980).

Male : female sex ratios were near 1:1 on most dates, but sample sizes were often small. Greatest departures from 1:1 were on 11 January (0.5:1), 27 July (0.3:1) and 18 August (2:1).

An unidentified dajid isopod was attached to the first pleonite of the 13 mysids collected. Parasitized mysids ranged in size from 1.0 to 2.2 mm CL. None of the other seven genera of mysids identified from Kuwait Bay and the Khor al Sabiya during this study (*Afromysis*?, *Dioptromysis*/*Kainomatomysis*?, *Erythrops* spp., *Mysidopsis*, *Proneomysis* and *Siriella*) were found parasitized. Most of these other taxa were quite rare with *Proneomysis* and *Siriella* the only other genera that were locally abundant.

Acknowledgments

Appreciation is extended to U. Jayusi of Dames & Moore for his support and to T. E. Bowman for verifying the identity of *R. tattersallae* and identifying the other mysid genera.

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Fig. 5. Distribution of *Rhopalophthalmus tattersallae* brood sizes by season in the Khor al Sabiya, Kuwait, September 1981–1982.

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PYCNOGONIDA OF THE WESTERN PACIFIC ISLANDS VI. *SERICOSURA COCHLEIFOVEA,* A NEW HYDROTHERMAL VENT SPECIES FROM THE MARIANAS BACK-ARC BASIN

C. Allan Child

Abstract.—A new species, *Sericosura cochleifovea,* is described from sixteen specimens taken by the Research Submersible *Alvin* in 3660 m at the hydrothermal Snail Pits Vent, Burke Field, in the Marianas Back-Arc Basin. The new species is compared with the two other known species of this genus and their distribution is discussed. The generic diagnosis is emended to include variation in palp segment numbers from seven to nine.

There are only two reports (Child 1987, Turpaeva 1988) on Pycnogonida taken from deep sea hydrothermal vents. With the increasing efforts expended in finding and investigating new vent fields, it is not surprising that additional pycnogonids have been and will be found. The new species described here was found during the exploration and sampling of recently discovered vent fields west of the Marianas Islands. These vent fields are part of a tectonic spreading zone investigated by scientists from Scripps Institution of Oceanography in April and May, 1987. The biological team of the group investigated three active vent sites along part of the spreading zone. Depths of the three sites varied from 3595 to 3660 m and are characterized by pillow basalts, hydrothermal mounds, vent chimneys, and many vent openings of both active and extinct vents. Fauna is dense in and around the vents with "hairy" snails, brachyuran crabs, bresiliid shrimps, and white anemones as the dominant observable fauna (Hessler et al. 1988).

The team collected a total of 17 specimens of a previously unknown pycnogonid from vent sites in the Snail Pits portion of Burke Field (16) and from the Alice Springs Field (1). Burke Field is dominated by dense aggregations of "hairy" snails that clog the vent openings. The temperature of the emerging water was 4–15°C, and the hot water venting from the openings was crystal clear. Water from Anemone Heaven vents nearby was cloudy. Alice Springs vent water was crystal clear.

Family Ammotheidae
Genus *Sericosura* Fry & Hedgpeth, 1969
Sericosura cochleifovea, new species
Fig. 1

Material examined.—Marianas Back-Arc Basin, Burke Hydrothermal Vent Field, Snail Pits vent site, 18°19.9′N, 144°43.2′E, 3660 m, coll. R/V *Alvin,* Dive 1835, 26 Apr 1987 (one male with eggs, holotype, USNM 234505, one male with eggs, one male juvenile, 4 female juveniles, paratypes, USNM 234506).

Other material: Dive 1835 (two males with eggs, four males, two females, one juvenile), Alice Springs Field, 18°12.6′N, 144°42.4′E, 3640 m, coll. R/V *Alvin,* Dive 1843, 4 May 1987 (one male juvenile).

Description.—Size moderately small, leg span 13.1 mm. Trunk moderately slender, fully segmented, posterior rim of anterior three segments flared out in cowl-shape, without dorsomedian tubercles or setae. Neck short, expanded anteriorly at palp in-

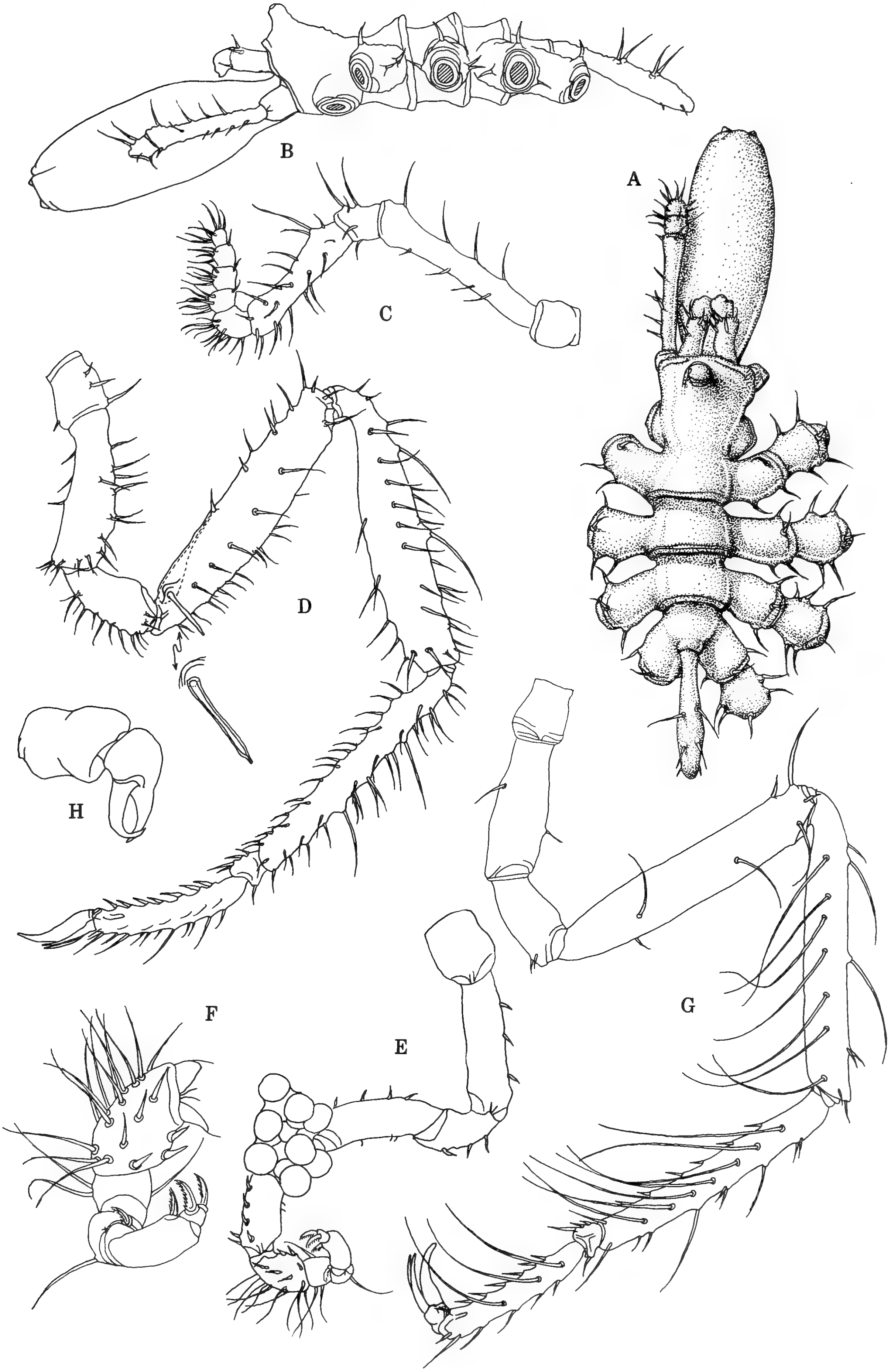

Fig. 1. *Sericosura cochleifovea,* holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Palp; D, Third leg, with cement gland tube enlarged; E, Oviger with several eggs attached; F, Oviger terminal segments, enlarged. Paratype female: G, Third leg. Paratype juvenile: H, Chelifore, enlarged.

sertion, without tubercles or setae. Ocular tubercle short, carried on elevated swelling at anterior of ocular segment, tubercle only slightly taller than basal diameter, rounded at tip, eyes lacking, sensory papillae prominent. Oviger implantation at posterior of neck, anterior to but not touching first pair of lateral processes. Lateral processes closely crowded, separated by half their diameters or less, 1.5 times longer than their maximum diameters, armed with stout dorsodistal spine on each, two posterolateral spines on anterior two pairs, single posterolateral spine on posterior two pairs, and anterolateral spine on posterior three pairs, spines half as long as segment diameters. Proboscis long, massive, without constrictions, carried horizontally, oral surface flat with slightly protruding lateral lips. Abdomen slender, slightly swollen distally, extending to midpoint of second coxae of fourth legs, with basal segmentation line, armed with two dorsal pairs of spines longer than segment diameter and pair of very short laterodistal setae.

Chelifores short, robust, two-segmented. Scape only twice as long as maximum diameter, armed with five to six short dorsodistal and laterodistal setae. Chelae small, bulbous, with scant trace of vestigial finger, without setae.

Palps nine-segmented, armed with few setae longer than segment diameter proximally, setae increasing in numbers on distal segments. Fourth segment only 0.75 length of second, third only slightly longer than fifth, distal four segments not longer than wide. Second and fourth segments slightly inflated distally.

Oviger second and fourth segments subequal, second through fifth segments armed with several recurved spines, fourth and fifth with few lateral setae, sixth with 3 endal recurved spines and field of 17–18 ectal setae longer than segment diameter, seventh with 3–4 similar setae, 8th with single seta. Short, finely serrate denticulate spines on terminal three segments in the formula 1:1:2. Eggs carried in round aggregations, size only slightly less than adjacent oviger diameter.

Legs moderately long, very setose. Setae arranged in dorsal, lateral, and ventral rows, some dorsal setae longer than segment diameter, others about as long as segment diameter, setae increasing in numbers distally. Longer dorsal setae arising from low tubercles. Second coxae almost equal in length to first and third combined. Femorae equal in length to first tibiae, second tibiae slightly shorter. Single femoral cement gland at extreme proximal end of segment, protruding as small bulge on anterior surface with a syringe-shaped tube as long as the segment diameter carried pointing dorsally. Bulge and tube invisible from posterior of leg. Tarsus very short, subtriangular, propodus slender, slightly curved, almost five times length of tarsus, armed with dorsal and lateral setae similar to those of tibiae. Sole armed with seven to eight short spines of similar size. Claw robust, half propodal length, moderately curved, auxiliaries about 0.7 length and with same curve as main claw. Sex pores on second coxae of posterior 4 legs.

Female and juvenile paratypes: female slightly larger in most measurements. Leg setation extremely dimorphic. Coxae with few short setae, femur with two long lateral setae per side, setae twice segment diameter, and single long dorsodistal seta. Tibial setae few on dorsal and ventral surfaces, row of seven extremely long lateral setae per side, up to five times segment diameters, propodus with three long lateral setae per side. Main and auxiliary claws slightly longer in relation to propodus than those of male. Sexual pores not evident on subadult females. Juvenile and subadult females with fully developed small chelae without teeth on scape of slightly smaller size than that of adult males.

Measurements.—Holotype, in mm: Trunk length (chelifore insertion to tip 4th lateral processes), 1.65; trunk width (across 2nd lateral processes), 1.04; proboscis length, 1.31; abdomen length, 0.72; third leg, coxa 1, 0.3; coxa 2, 0.64; coxa 3, 0.44; femur, 1.22; tibia 1, 1.22; tibia 2, 1.11; tarsus, 0.14; propodus, 0.65; claw, 0.32.

Distribution.—Known from the type locality, Snail Pits Vent in Burke Hydrothermal Vent Field, Marianas Back-Arc Basin, in 3660 m, and from Alice Springs Field in 3640 m.

Etymology.—The specific name is Latin (*cochlea* = snail, and *fovea* = pit) and refers to the collecting site.

Remarks.—This species is very closely related to another north Pacific species recently described, *Sericosura venticola* Child. The two species would be synonymous were it not for a set of small but taxonomically important differences which serve to separate them. Each of the differences taken individually would not be sufficient to designate this species as a new taxon, but the set of small differences in total are enough in my opinion.

The differences in this new species are: a palp of nine segments which have not coalesced into the seven of *S. venticola,* a much longer syringe-shaped cement gland tube, a slightly shorter neck with the oviger implantation slightly more anterior, dorsodistal spines on the lateral processes and posterolateral spines placed more proximally, a shorter abdomen bearing a different spine arrangement, a much shorter fourth palp segment, a longer fourth oviger segment in relation to the second and many more long setae and a different denticulate spine arrangement on the terminal segments, different coxal length ratios and many less ventral setae on the third coxae and proximal femorae of the holotype, and different major leg segment ratios (femur = first tibia in this species while femur = second tibia in *S. venticola*). The new species is only half the size of *S. venticola.* While this fact is of little or no value itself in separating species, it contributes to the suite of differences which determine this new species.

The chelate subadult females of the type lot contribute to the known sexual dimorphism feature of this genus. The first species known in this genus, *Sericosura mitrata* (Gordon), is also quite closely related to the two other species and has sexually dimorphic features best seen in the legs, as in the new species. Gordon's species has male legs with relatively few long dorsal and lateral setae while the female legs have many short ventral spines or setae on the major segments along with many very long slender ventral setae on the tibiae. The new species male legs have many dorsal, lateral, and ventral setae of various lengths while the female legs have far fewer of these setae while having many extremely long lateral setae not found on legs of the male. The legs of *S. venticola* have a ventral field of many moderately long setae on the third coxae and these extend to the proximoventral femur opposite the dorsolateral cement gland. Unfortunately, the female of the latter species remains unknown along with whatever dimorphism exists for this species.

Discussion

The three species of *Sericosura* present an often encountered distributional problem among the pycnogonids. The first species to be described, *S. mitrata* (Gordon 1944:54–57, figs. 19a–e, 22b), was found on the coast of Antarctica in slightly over 200 meters, and was subsequently found on the Walvis Ridge off southern Africa in well over 2000 meters (Child 1982:19–21, fig. 6). The second known species, *S. venticola* Child (1987: 896–899, fig. 2; *Scipiolus thermophilus* Turpaeva=), is from the Juan de Fuca Ridge hydrothermal vent fields in depths of slightly more than 2200 meters. This new species, *S. cochleifovea,* is from the opposite side of the Pacific at the Marianas Back-Arc Basin in the deepest waters known for the genus, 3660 m. It would be convenient to state that the genus is hydrothermal vent-related except that we know nothing about the two collecting localities for *S. mitrata.* No hydrothermal activity is known for the Walvis Ridge locality but it would be surprising to find hydrothermal vent activity in less than 300 meters of depth off the coast of Antarctica. The three known species are found in widely disparate localities suggesting that the genus is worldwide in distribution but the species undoubtedly are much more restricted, as with almost all pycnogonids, to specific areas and are in most cases associated with zones of tectonic spreading having hydrothermal vent fields.

The other anomaly among the three species is the discovery of this new species bearing nine palp segments. The other two species have seven with the three distal segments now appearing to have coalesced from a larger number, presumably nine. Other genera such as *Achelia, Tanystylum, Ammothea,* and others, have groups of species with palp segments varying in segment numbers, so the feature is not a new discovery except in this genus. The generic diagnosis therefore needs to be revised to include palps having seven or nine segments instead of the previously diagnosed seven.

The genus *Ammothea,* from which this genus presumably split, has palps of eight or nine segments. This seven and nine palp segment character of *Sericosura* places it nearer the diagnosis of *Ammothea.* The only remaining major differences between these genera are the lack of a row of dorsomedian tubercles on the trunk of *Sericosura* species and the shape and placement of the cement glands and tubes. Most of the species of *Ammothea* have conspicuous dorsomedian tubercles on the posterior trunk segment ridges while none of the three *Sericosura* species are known to have these. The cement glands and tubes in *Ammothea,* where known, are placed at the dorsodistal tip, or nearly so, of the femorae and are inconspicuous. The fact that the cement gland and its conspicuous bulge and tube is placed proximally on the anterior of the femorae in *Sericosura* is probably a sufficient reason to maintain the genus as separate from *Ammothea.* The leg setae dimorphism and other lesser characters only reinforce the separation of this genus from the closely related *Ammothea.*

Acknowledgments

I am grateful to Dr. Robert R. Hessler, Scripps Institution of Oceanography, La Jolla, California, for bringing the specimens to my attention, supplying excellent data concerning their collection, and for donating the specimens to the National Museum collections. Investigations of the Marianas Back-Arc Basin and the collection of specimens by Dr. Hessler and Dr. Harmon Craig were supported by NSF grant OCE83-11258, for which appreciation is herein expressed.

Seven type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, under the catalog numbers of the old U.S. National Museum. The other specimens have been returned to the Scripps Institution of Oceanography, deposited in the Los Angeles County Museum, California, the National Museum, Paris, and several added to the non-type collections at the National Museum of Natural History, Washington, D.C.

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A NEW SPECIES OF THE CAMBARINCOLID GENUS *SATHODRILUS* FROM MISSOURI, WITH THE PROPOSAL OF A REPLACEMENT NAME FOR *ADENODRILUS* HOLT, 1977 (CLITELLATA: BRANCHIOBDELLIDA)

Perry C. Holt

Abstract.—*Sathodrilus nigrofluvius* is described and illustrated. Its relationships, distribution and possibly primitive status within the genus are described. *Uglukodrilus* is proposed as a replacement for the preoccupied name *Adenodrilus* Holt, 1977.

The description of a new branchiobdellidan presented below is offered as a part of an ongoing effort to describe the members of the genera *Oedipodrilus* Holt, 1967, and *Sathodrilus* Holt, 1968, from the southern Appalachian and Ozarkian regions of the southeastern United States. In addition, this opportunity is taken to propose a replacement name for *Adenodrilus* Holt, 1977, a junior homonym.

Sathodrilus nigrofluvius, new species
Fig. 1

Type specimens.—Holotype, USNM 118199, and three paratypes, USNM 118200–118202, taken from a tributary of the Black River, 2 mi NE of Lesterville, Reynolds County, Missouri, on State Road 21, on unknown host, 22 Aug 1961, by Perry C. Holt.

Diagnosis.—Slender, small worms (holotype 1.7 mm in length); dorsal ridge on segment VIII; lips entire; no oral papillae; jaws slight, triangular in lateral aspect, very light in color, dental formula (?) 5/4; one prominent pharyngeal sulcus, no corresponding exterior one; bursa large, approaching diameter of segment VI in length, penial sheath greater in diameter than atrial region, penis a straight, cuticular, eversible tube; ejaculatory duct short, slender, thin-walled; spermiducal gland without prostate or prostatic protuberance or deferent lobes; spermatheca with thick ectal duct, median bulb, ental process.

Etymology.—Latin, Black River.

Description.—The members of *Sathodrilus nigrofluvius* are small and relatively slender worms. The holotype and four paratypes have the following mean dimensions: total length, 1.6 mm; greatest diameter, 0.3 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.2 mm.

The lips are entire and there are no oral papillae. The eighth body segment bears a low, but distinct dorsal ridge, the others lack dorsal supernumerary muscles. The head tapers slightly towards the peristomium. The clitellum, on segments VI and VII is distinct but not prominent. The anterior nephridiopore opens dorsally on the anterior margin of segment III.

The jaws are small, about one twenty-fifth that of the head in length, delicate, light in color. The dental formula appears to be the common one of 5/4, but the teeth are small, uncolored and difficult to detect. The paucity of material (the types) makes it inadvisable to destroy it in order to verify this point.

The gut contents consist of detritus and diatoms.

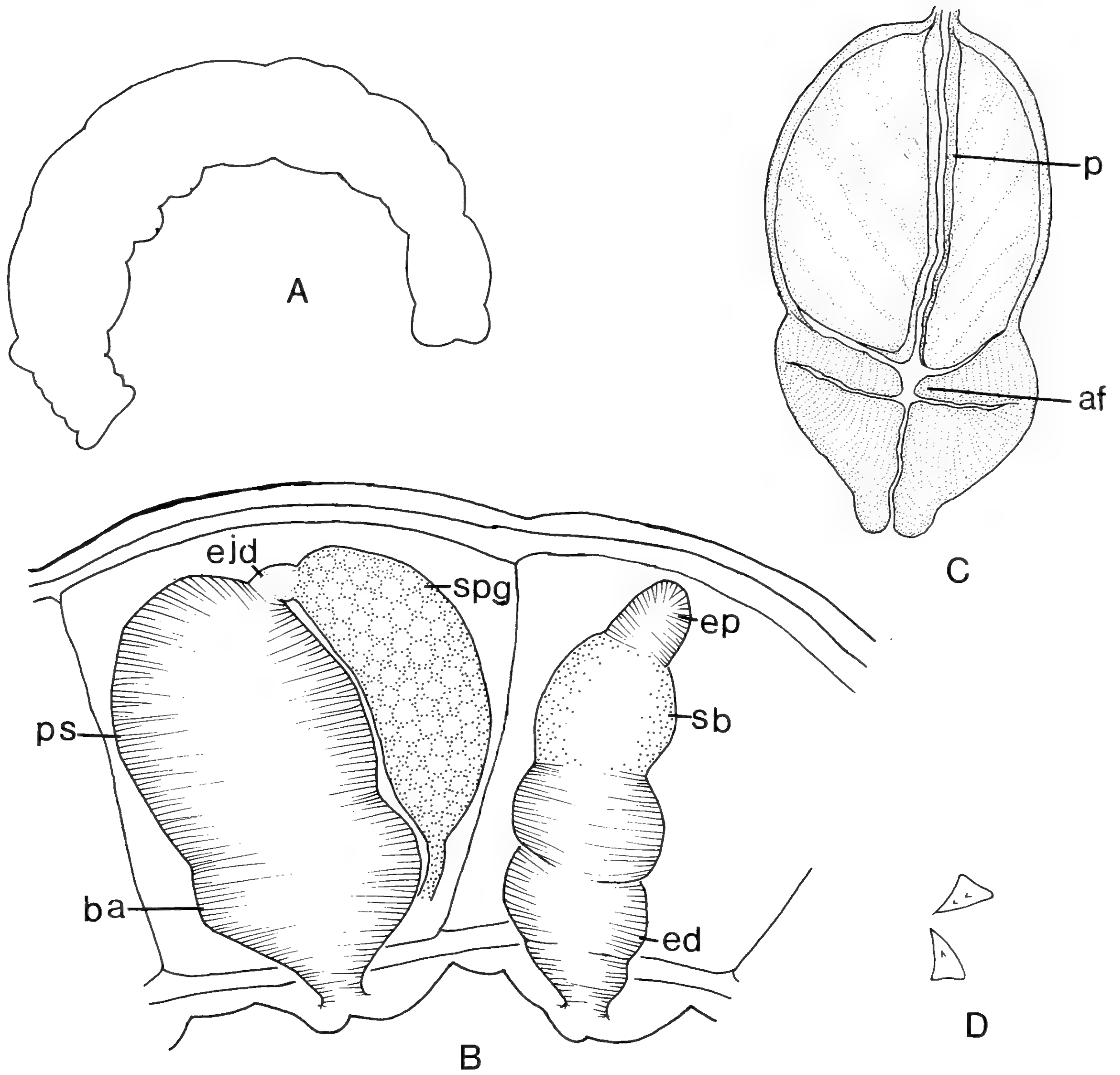

Fig. 1. *Sathodrilus nigrofluvius*: A, Lateral view of holotype; B, Lateral view of reproductive systems of holotype; C, Optical section of bursa; D, Lateral view of jaws. Abbreviations: af, atrial fold; ba, bursal atrium; ed, ectal duct of spermatheca; ejd, ejaculatory duct; ep, ental process of spermatheca; p, penis; ps, penial sheath of bursa; sb, bulb of spermatheca; spg, spermaducal gland.

The spermiducal gland lacks deferent lobes, is about two-thirds the diameter of segment VI in length and three-eighths its own length in diameter and is slightly tapered at each end. It lacks even the rudiment of a prostate, and often lies longitudinally above the gut.

The ejaculatory duct is a short, thin-walled, obscure tube that is more nearly inferred than seen in the available specimens. In one paratype it appears to be greatly expanded and the penial sheath collapsed at the place of its entry into the latter. Since serial sections are unavailable, it is possible, but unlikely, that the spermiducal gland opens directly into the penial sheath region of the bursa.

The bursa is a cylindrical sac, subequal to the body diameter in length. About one-third of its length consists of the atrium and atrial fold with a greatly reduced lumen. The penis is a straight, cuticular tube attached by relatively thick strands to the inner wall of the penial sheath which is set off externally from the bursal atrium by an encircling constriction (Fig. 1C).

The spermatheca is characterized by a thick, muscular, irregularly bent ectal duct that constitutes at least one-half the total length of the organ, a relatively short spermathecal bulb that is no greater in diameter than the ectal duct and a short, narrowed ental process (Fig. 1B).

Variations.—In one specimen the anterodorsal quadrat of the bursa is collapsed and the ejaculatory duct may be greatly expanded. Otherwise, no differences were noted.

Affinities.—Among the species presently assigned to the genus *Sathodrilus, S. veracruzicus* Holt, 1968; *S. hortoni* Holt, 1973; *S. okaloosae* Holt, 1973; *S. shastae* Holt, 1981; and *S. nigrofluvius* lack a prostate or rudiment thereof (i.e. how many do have a prostate; how big is this genus?). Of this coherent group, *S. nigrofluvius* most nearly resembles *S. veracruzicus.*

Unlike *S. nigrofluvius, S. veracruzicus* lacks dorsal ridges, appears to have oral papillae, and has a proportionately shorter and more slender spermiducal gland, a longer and more slender bursa, a penis that is looped (and hence longer than its sheath), and a spermatheca with an ectal duct that is less in diameter than the spermathecal bulb and lacks an ental process.

Sathodrilus hortoni consists of larger worms with a parasitic mien: a thin body wall and a gut filled with "globules of fat." The "oesophagus" is attached by strands of muscle to the body wall of segments I and II (Holt 1973:97–98). The upper lip is lobed. The secondary reproductive organs are unusual: the male efferent apparatus is proportionately small, the spermiducal gland relatively long and slender; the spermatheca is composed of a large muscular spermathecal bursa and a slender spermatozoa storing "bulb" with a thick muscular wall and no ental process.

Sathodrilus okaloosae has low dorsal ridges on the body segments. The jaws are unusual: broad and thick with a "dental ridge" bearing the teeth and a dental formula of doubtfully 3/4, possibly 1/4 (Holt 1973:101). The bursa is less than the body diameter in length. The spermatheca has a long, slender ectal duct and a long ental process, both proportionately less in diameter than those of *S. nigrofluvius.*

Sathodrilus shastae is composed of larger animals up to 4 mm in length with two pharyngeal sulci and no dorsal ridges. The jaws are prominent; the dental formula 1/1. The ejaculatory duct is long and thick and the spermiducal gland is remarkably long (about twice the body diameter in length) and slender. The bursa, including penial sheath and penis, is proportionately small. The ectal duct of the spermatheca is short, the ental process narrow, the median bulb fusiform and flattened between the gut and body wall.

Host.—Unknown.

Distribution.—Members of the genus are distributed widely over the continent, but it may be worthy of note that the most structurally similar relative of *S. nigrofluvius* is from southern Mexico (the state of Veracruz) with its other close relatives from Florida (two) and the Pacific northwest, a distribution that suggests, as does the absence of a prostate, that these species are "among the least dervied" within the genus.

Material examined.—The types.

Dr. Stuart R. Gelder has informed me that the name *Adenodrilus* which I proposed (Holt 1977) for a genus later (Holt 1986) assigned to the family Bdellodrilidae is a junior secondary homonym of *Adenodrilus* Chekanovskaya, 1959, based on a haplotaxid oligochaete from central Asia.

The genus-name *Uglukodrilus* is hereby proposed as a replacement name for *Adenodrilus* Holt, 1977. It is to be considered as masculine and is derived from that of the leader of a fictional band of Orcs (see Tolkien, J. R. R. The Lord of the Rings, v. 2, 1954) whose feeding habits were considered suspect.

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As always, I am grateful. Also, I wish to thank Dr. Stuart R. Gelder for calling to my attention the homonymy of *Adenodrilus* Holt, 1977. Dr. Ernest R. Stout, Head, Department of Biology, Virginia Polytechnic Institute and State University, and his secretaries have been unsparing in their support and help of which I am greatly appreciative.

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THE SECOND ANNUAL RISER LECTURE: ECLECTICISM AND THE STUDY OF POLYCHAETES

Kristian Fauchald

Abstract.—The study of polychaetes has involved two very different research programs: the morphological and systematic descriptions on one hand and the biological and physiological traditions on the other hand. The two traditions each represent two systems of two different approaches to the study of nature: on one hand structural versus procedural studies and on the other hand process-oriented versus taxon-oriented studies. None of the paradigmatic approaches common in biology (e.g., ecological, physiological, genetic or evolutionary) can solve their own problems by using only one of the four approaches. Understanding the biology of the group can only come from a carefully managed eclectic approach to the study of the group.

During the early part of my career the theory of science always appeared to exist totally independent of what I was doing as a biologist: Biology was something to be done, not thought about. A paper published about 25 years ago (Platt 1964) demonstrated that I had been very wrong; the quality of a study depends crucially on the manner in which it is planned and performed.

Since then I have examined my own and my fellow workers output for signs of an awareness of theoretical issues associated with the study of biology. I have concentrated on the polychaete literature with which I am most familiar. By now more than 200 years worth of papers on polychaete morphology, systematics, phylogeny, physiology and ecology have accumulated, representing more than 10,000 individual papers and books.

In this paper I will review, very briefly, the development of the study of polychaetes. I will then attempt to put this overview into a minimal theoretical context. The results are some rather trivial admonitions. I believe these recommendations to be worthwhile because most of my colleagues still behave as if their activities were theory-independent. If I can set them thinking about these issues, then the purpose of this paper will have been fulfilled.

Early Studies of Polychaetes

Aristoteles reported what might be interpreted as scaleworms in the ocean; Pliny the Older gave a much more convincing description of "marine scolopenders" (Gillet 1988) and this latter report was expanded on by both Rondelet and Gesner (Williams 1851); these "scolopenders" have traditionally been identified as nereidid polychaetes. For all practical purposes polychaetes were first described in 1758 in the 10th edition of Linnaeus Systema Naturae. These early reports and the transition into a scientific

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The Riser Lecture Series.—In 1985 the annual Riser Lecture was initiated by members, alumni and friends of the Marine Science Center, Northeastern University at Nahant, Massachusetts. The occasion was the official retirement of Professor Nathan W. Riser. As teacher, biologist and founder of the facility, "Pete" Riser endowed the laboratory with a legacy—the importance of considering the whole organism regardless of one's special focus. We dedicate these annual lectures to that principle.

study of the polychaetes is described by Gillet (1988).

Names and descriptions.—The Linnean nomenclature separated names as labels from descriptions and definitions of the organisms studied. For the first time logical procedures known since antiquity could be applied to the description of the living world. One could name an organism and define that label by descriptive terms, independent of the names themselves. The process has been taught as part of introductory classes in logic for a long time, nevertheless, the importance of this first application to biology was overwhelming. The new nomenclatural system made possible intelligible discourse about Nature in a way that no other device, before or after, has done. The practices of the scientists of the period reflected an awareness of the different language levels involved in descriptive processes (Popper 1979). For example, I believe that the use of names of gods and goddesses for genera of various organisms reflects an awareness of the importance of the separation of names from definitions and descriptions. The trivial names, what we now call the species names, often were simple mnemonics: *Nereis virens* for example: the green nereid. *Nereis diversicolor* is another example of this naming tradition.

The descriptions and definitions included morphological features. Microscopes were so primitive that not much more than gross morphological features could be distinguished. However, early illustrations may be remarkably accurate and detailed. Written descriptions uniformly are far less detailed. The early zoologists did exactly what we do: Include sufficient detail to distinguish new taxa from previously known ones. One can hardly blame Linnaeus and his contemporaries for not appreciating how many different kinds of worms would eventually be found, or for not developing the complete terminology for describing their wealth of morphological detail. The first major describers of polychaetes were Danes, Otto Friedrich Müller (Müller 1776) and Otto Fabricius (Fabricius 1780), Russians, such as Peter Paul Pallas (Pallas 1766) and by the turn of the century the famous French scientists Cuvier, Lamarck, and Savigny.

Reviews and classifications.—Lamarck and Cuvier, independently and in competition, reviewed all polychaetes described, sorted out, and named a whole series of new higher taxa, especially genera and families (Lamarck 1816, Cuvier 1817). Another famous French worker, Savigny, had made most of the new observations and descriptions. He was a careful observer with a fine eye for finding differences among similar forms (Savigny 1820). Lamarck added considerably to our understanding of the relationships among the polychaetes. Also his separation of the polychaetes into two major groups, those with red blood and those with white blood, revealed an interest in physiological properties of the organisms. Nevertheless, more of Cuvier's morphology-based system has been retained than of Lamarck's.

Detailed descriptions of newly discovered polychaetes became divorced from the time in which they were penned. The descriptions have increased in detail and length from one or two lines to several printed pages, but we still use most of the terminology and the overall pattern of descriptions established by Audouin and Milne Edwards in a study of the French fauna in the early 1830's (summarized in Audouin & Milne Edwards 1834).

The system used by Audouin and Milne Edwards closely resembled the Cuvierian system and formed the base for all workers over the next 20 years. By 1850 however, the emphasis of exploration shifted to Germany: Adolph-Eduard Grube (1850) issued a major review of the polychaete families and this paper was the standard for the next 15 years.

Two scientists working in Stockholm made the next major advances in the mid 1860's. Kinberg reported on his worldwide travels and Malmgren detailed the North Atlantic and Arctic Ocean faunas. These two scientists represent two very different approaches to descriptive science. Kinberg briefly described species collected on the cruise of the *Eugenie* around the globe and added numerous new taxa at all levels (Kinberg 1865, 1910). Malmgren's (1867) studies were intensive; he focussed his attention on a much smaller area and carefully reviewed all previous work before committing himself to describing a new taxon. This difference in approach closely matches a perennial difference among descriptive biologists; among modern systematists Gesa Hartmann-Schröder and Olga Hartman both have used Kinberg's approach, whereas Marian H. Pettibone more closely matches Malmgren. I have done a bit of both.

Kinberg and especially Malmgren did their best to increase the consistency in use of terms and in the amount of detail required for adequate descriptions. Quatrefages (1866) issued a large-scale review of the whole annelid fauna as he knew it. Perhaps more pedestrian a systematist than the others mentioned, he nevertheless became extremely influential, due in part I believe to his location: he was in Paris, and had a long history of publications on polychaetes by the time he issued his magnum opus. Kinberg had published a few earlier papers, but neither he nor Malmgren ever issued any additional major contributions to the study of polychaetes. They both left science shortly after the papers mentioned were published.

Ludwig Schmarda is one of the more colorful persons in the history of polychaete studies. He travelled around the world in the 1850's, not in an exploring vessel, but by hitch-hiking on commercial sailing vessels. His description of his trip from South Africa to Australia is singularly harrowing, including very bad weather, seasickness, scurvy and assorted other diseases. In Chile he lost his collections to a fire on board; in Panama he was robbed by some rather unsavory characters who made their living by preying on people going from the U.S. east coast to the west coast via the Isthmus. Despite the loss of his collections, he published a large report (Schmarda 1861) that apparently was largely overlooked by his contemporaries. This was probably in part due to the increasing standards of descriptions and illustrations. Schmarda's effort was, however, the earliest worldwide tropical survey of polychaetes. He described a large number of new species for which there are few types available and poor locality information. At that time, there was no requirement that types should be deposited anywhere: Descriptions were considered adequate evidence for the presence of a new taxon. However, the first Nomenclature Code, and perhaps just as importantly, the first volume of Zoological Record, was issued in 1864.

The morphological tradition.—The morphological tradition, outlined above, has continued through the work of McIntosh (1885), Fauvel (1923, 1927), and Augener (1918), and is now followed by most practicing systematists. The total focus of this tradition is very limited in the kind of evidence deemed acceptable. Most systematists will accept only features that can be seen either with the naked eye or with stereo or compound microscopes as valid taxonomic characters. Furthermore, a tradition among polychaete systematists suggests that all reasonably well preserved specimens, especially anterior ends, should be identifiable to species. I have more than once heard complaints from well known systematists that a published description was too difficult to use, or was impractical, because it used information not readily available using minimal technical equipment, or required the presence of complete specimens. This tradition is clearly at odds with, for example, students of isopod crustaceans who for years have accepted limits on the identifiability of all specimens.

The biological tradition.—Another tradition in the study of polychaetes dates back to about 1850. Thomas Williams (1851) published a major review of the biology and physiology of the polychaetes. This summary is now rarely quoted; it has been superceded by more recent reviews, but it was important historically because Williams reviewed all information available about the life of all worms known to science. Some of the data quoted by Williams date back to Lamarck and are speculative rather than observational in nature and some rather quaint notions were paraded only eight years before the publication of Darwin's Origin of Species. Williams made some original physiological observations on various English polychaetes.

The most impressive of the early polychaete biologists was Eduard Claparède, a rather tubercular-looking Swiss, who did most of his work in France and Italy (Claparède 1854). By 1865 he had gotten into a rather virulent quarrel with Quatrefages over all of Quatrefages' new taxa, defined in many cases without access to any material (Quatrefages 1865a, Claparède 1865, Quatrefages 1865b). Claparède emphasized the importance of observations on live organisms; Quatrefages by that time had become very collections-oriented. This difference in approach formed the background for the disagreement. Claparède, true to his principle, deposited no specimens in any museum, making many of his new taxa difficult to define accurately.

The second tradition was biological in nature: studying live organisms and making observations of the live processes, such as reproduction, development and feeding. These kinds of observations were difficult to quantify in an age of poor mechanical recording devices, no photography to speak of, and certainly no electronic recording devices. Additionally, statistics had not yet developed to the point where repeated samples were taken. The studies were therefore often episodic in nature, and observations were only rarely organized into tables or other means of presenting large, easily surveyed data. The kinds of observations attempted by Claparède are still difficult to document for theoretical reasons that I will touch on below.

Claparède combined his studies of live organisms with a detailed study of microanatomical structures. These studies are excellent and are still the best starting point for any anatomical studies in the groups he covered. Claparède's illustrations are among the best ever published on polychaetes. The most important aspect of Claparèdes work was that he demonstrated that a remarkable amount of information could be gained by looking at live organisms. He also demonstrated that detailed anatomical and histological studies yielded systematically distributed information, which could be potentially useful in systematics.

Ehlers tried to combine the two traditions in his massive publication "Die Borstenwürmer" issued in two parts (Ehlers 1864–1868). Some of his descriptions of new taxa run 10–15 printed pages, accompanied by one or two full packed plates of illustrations. Consequently, Ehlers succeeded in going through less than ⅓ of the then known polychaete taxa in roughly 700 pages of text, but for the groups he covered, his volume is absolutely indispensible. Ehlers' research later devolved to thoroughly traditional, morphological descriptions. I can find no evidence in any of his publications that he attempted to complete the massive study he had started.

The study of live polychaetes eventually developed into a tradition of physiological studies, based usually on members of relatively few families with highly characteristic, often unusual physiological patterns. These studies are often performed by process-oriented rather than by comparative scientists. Reproductive studies, while covering in part members of most groups, have been focussed on eunicids, nereidids and syllids (Schroeder & Hermans 1975); studies of respiratory and blood physiology on glycerids, terebellids and scattered other groups (Dales 1969, Florkin 1969). Studies of regeneration have focussed on sabellids with few glances in other directions (Needham 1969). Genetic studies have been done on dorvilleids and little else (Åkesson 1982). Neurophysiologists have studied the properties of the giant nerve fibers in sabellids of the genus *Myxicola* with very little concern for the biology of the organism at all. There are about 80 families of polychaetes and of these at least 60 are common in shallow water and relatively readily available; nevertheless live studies have focussed on a few popular groups and usually on only one or a few species in each group at that.

The results of the biological and physiological studies have been very valuable, but less as a comparative study of polychaetes than as an exploration of various biological and physiological mechanisms.

Theory and the Study of Polychaetes

The rather conservative descriptive tradition continues among polychaete systematists; for each advance in morphological or anatomical technique, traditionalists hang back, not wanting to get involved with new methods or add new features to the descriptions. Often the young turks among polychaetologists are traditionalists in the study of other groups of organisms, especially vertebrates. Very few of the scientists closely associated with the study of polychaetes have demonstrated strong theoretical interests. For example, it is difficult to find any reference to evolution, or to Darwinian or anti-Darwinian thinking anywhere. Ehlers' publication from 1864–1868 gave no indication of a major revolution in biological thinking taking place at the time. McIntosh (1885) mentioned nothing about phylogeny in his treatment of the *Challenger* polychaetes. One outstanding exception is E. Meyer, who in his studies of polychaetes indicated a good, often anticipatory understanding of biological theory (Meyer 1890). This paper is frequently quoted in the literature on phylogeny of the invertebrates, but not often by polychaete taxonomists.

Some of the developmental biologists associated with the study of spiral cleavage at Woods Hole Marine Biological Laboratory used polychaetes for their studies. These scientists had deep theoretical interests and showed great skill in using the polychaete material in clarifying theoretical problems (Wilson 1898, Treadwell 1901).

The reason for the lack of theoretical and one might say scholarly interest in the study of polychaetes is relatively easily found. Most scientists published only a single paper on polychaetes and very few made the study of these animals their lifetime occupation (Reish 1958). Through about 1950, the study of polychaetes was a relatively leisurely pursuit. Even in most early benthic ecology studies (Petersen 1911, Blegvad 1930), few polychaetes are mentioned or named, except to family. In morphological studies, the annelids were considered a stepping stone to the arthropods (Hanström 1928, Binard & Jenner 1928, and the discussion of the anterior nervous system of the annelids and arthropods) and thus of interest insofar as they showed the step-wise advance to the conditions present in the arthropods. Parenthetically, papers that treat polychaetes well from a theoretical point of view were, with few exceptions, written by scientists with a limited experience in the group (Hanström 1928, Hatschek 1893). This generalization is far less true today than it was before WWII.

The rapid development of interest in benthic ecology following the publication of Thorson's (1957) review of the topic lead to considerable change in attitude. Polychaetes have turned out to be extremely common in the marine benthos; benthos ecologists have changed their attitudes towards the importance of polychaetes with the mesh-size of their screens. Further, modern ecologists are aware that no questions can be answered by studying only a few "representative" organisms, usually selected among "easily identified" organisms, such as some crustaceans, echinoderms and mollusks, as done in the early days of benthic ecology.

Simple thoughts on theory.—Organisms may be studied in four different ways, which may be organized into two systems of two. First, one may either attempt to describe the structural characteristics of an organism, or one may study interactions among structures in time or space. The other system of classifying observations describes the investigational intent. One may study the same process in a variety of organisms; or, alternatively, one may study a variety of processes and structures in the same kinds of organisms.

Structural descriptions historically started with external morphology, and proceeded via internal anatomy to microscopic anatomy in all its phases. Structural descriptions deal with the material presence of anything, including atoms and subatomic particles. In gross morphological descriptions the unaided eye is used; all other descriptions are based on interpretation of images created by various pieces of gear: microscopes of all kinds, meters and dials and color-reactions, spectrophotometers, or small patches of color on a starch gel. The more highly magnified the analysis becomes, the more remote the interpretation of the findings become from normal human experiences, but, at least in theory, no different from observations of gross morphology. In some sense, interpretation becomes easier with increasing magnification, since the higher magnification allows a far more precise use of language in describing limiting conditions than do observations of a morphological or anatomical nature.

Natural historians and some physiologists (a subgroup of the comparative and ecological physiologists) seek a completely different kind of information about organisms, information which we have had a great deal of difficulty entering into our structurally derived patterns. All organisms change with time and all structural landmarks change in relation to each other during ontogenesis, presumably in an organized fashion, but not necessarily in the same pattern even in genetically similar organisms. Information derived from these changes is as much an expression of the genome of the organism as is the structural information. I am aware of the problems including this kind of information in our descriptions will create, but I believe that until we do, we will fall short of understanding the organisms we are studying. Computerized modelling may offer help in creating testable predictions for such studies.

The other system of groupings of study is familiar to most scientists, especially in technically more complex fields. Scientists become experts on the use of a single technique: transmission and scanning electron microscopes, enzyme electrophoresis, DNA hybridization and so forth and will investigate the limits of what the technique can do. The results of this approach have been excellent and have lead to major advances in our understanding of microstructures and various processes.

The other major way of looking at the organisms is as a specialist on a single animal group; a taxon-oriented person. Such a person may be eclectic in their use of techniques, but will rarely add to the development of new techniques. These biologists often have a better understanding of the evolutionary significance of differences in processes among the organisms studied than the process-oriented scientists, but are usually rather parochial in their view of the world. A polychaete's-eye view of the globe is limiting in many ways.

These four ways of studying organisms do not agree with the traditional breakdown of specialities among biologists. Taxonomists, while primarily concerned with description of structure, frequently resort to adaptive explanations. Physiologists, while exploring functional issues, base themselves in knowledge of the structures involved in the particular processes studied. Perhaps most confused are the activities that are now subsumed under the heading of ecology. In part, ecologists describe structure in their case patterns of distribution of organisms in nature, but usually use functional explanations for the patterns demonstrated. The separation of the two modes of thinking is not trivial, but is built into the language. Ideally a language describing structure should use only shape and position words; in practice we use such words as "branchiae" and "notopodial cirri." For trained taxonomists and morphologists the usual meanings of these words have become trivial: they are using both words as shape and position markers. However, notopodial cirri, usually slender, often very long cirri projecting from the dorsolateral sides of the worms, often appear to be as much respiratory as sensory in function.

Eclecticism and the study of polychaetes.—Thus an adequate description of any polychaete would require a rather eclectic collection of pieces of information, both static and dynamic.

Most structural descriptions of polychaetes now include a minimal mention of major morphological features. At least one species of most families have been studied anatomically, at least at the light microscope level. Very few truly comparative studies have been performed within each family. Comparative studies among the families are rather common, but without knowledge of how much variation to expect within each family, the interpretation of such comparative studies will always be difficult. Microanatomical studies are becoming rather more common, but again, with some very salutary exceptions, have focussed more on the relations among the families. Other studies, with both structural and functional components, are mentioned below.

Studies of comparative physiology have given us important information about the interactions among the structures, e.g., studies of mechanisms of respiration among polychaetes. However, most physiological studies have been focussed more on elucidating process and are for that reason usually not very useful for comparative purposes. Most life history studies published so far include an account of parts of the larval development and metamorphosis into a postlarvae, but little about the rest of the life of the organisms, including longevity (Fauchald 1983). The bits we have are interesting, but are insufficient for all species.

I am advocating eclecticism because I believe that this approach will force us to change our approach to our studies. Currently we learn one, or perhaps a few, techniques and then proceed to apply these to all problems, whether the application can solve the problems posed or not. The investigative technique and the detail sought must depend on the question asked, rather than the other way around. For example, it is not always useful or necessary to identify organisms to the species level in a benthic investigation. The first step in planning a study therefore must be to question the purpose of the investigation. If the purpose is an exploration of the area—a study of which organisms are present in what quantities—then identification to species is not only desirable, but the only way such information should be presented. But if the purpose is to investigate feeding biology or perhaps trophic structure, in addition to giving a listing of taxa present, at the very least as much effort must be put into investigation of gut contents and mechanisms of feeding, as into the identification of the specimens. Most investigators now identify their organisms (more or less accurately) and then quote some authority for the other information needed, e.g., feeding physiology. For the polychaetes, most quote Fauchald & Jumars (1979), an inappropriate source of information for this purpose. The Diet of Worms was written as a summary of what little information was available in the mid 1970's and was intended to spur investigations: It has apparently done so, but sufficient information is still not available for any species to my knowledge.

Polychaetes are valuable for a variety of studies. Polychaetes are ubiquitous and common in all marine environments. The numbers of polychaete taxa is large enough to allow the use of the statistical data reduction, but is not as overwhelming as in some other groups. Most major subgroups have morphologically very strict body plans and can be identified to family by rank tyros.

The group is very old (Fauchald 1984) and the major body plans were laid down a long time ago: We can in the polychaetes investigate current evolution of ancient body plans. For example, the eunicids are very uniform in general morphological appearance; in fact, the jaws have not changed much since Palaeozoic times. Nevertheless, a preliminary numerical study of about 300 individuals of approximately 12 species (Fauchald 1989) demonstrate several different patterns of growth and of control of the body proportions, implying rather different physiological properties, perhaps related to the maximum absolute size of each species.

The consequences of the studies of Grassle & Grassle (1976) and Eckelbarger & Grassle (1987), to mention only two of a series, are fascinating. They have given us a view of a worldwide group of small, ever-changing populations of capitellids becoming isolated, perhaps going extinct locally, perhaps meeting up again before, or after, completing a speciating process—in short, a complex mosaic.

Chromosome studies of various polychaetes indicate that ploidy relations may play a more important part in evolution in polychaetes than previously expected; perhaps leading to a reconsideration of the importance of the various processes in the evolution of animals.

An eclectic approach may thus complete the transformation of the study of polychaetes from an intellectual backwater to the forefront of biology.

Some final notes.—I agree with my alter ego of 25+ years ago that theory of science exists with little reference to what I do on a day to day basis. I have come to the realization that this is perhaps the way it ought to be. If the theory of science was strictly a description of what scientists do, then one could not expect discussion of normative rules. We all use theoretical constructs in even the simplest observations. The belief in theory-independent observations appears now on the wane. Philosophers of science study and perhaps build into systems the theories behind our observations and make us as working scientists aware of these constructs. Without the precision in thinking and data definition theory enforces, very little advance is possible.

A significant fraction of current papers are routine descriptions of a few new taxa, usually with a review paper as authority for the separate status of the new taxa; the material examined is minimal and comparison with types of previously described species is rare. If current theory and methods were applied to these studies, I am convinced that the deluge of new taxa would slow down. Most of the new taxa are collected during quantitative investigations and the authors do not have the luxury of performing a complete and detailed review of the family or genus of interest before publishing a new taxon or two. Detailed and rigorously performed reviews of previously described taxa are lacking for nearly all polychaete families and very few are now on the horizon. Most of the investigations in which the bulk of new material is collected have poorly, or inappropriately defined, goals; however, one requirement runs through most of them: No matter what the stated purpose of the investigation is, the organisms collected must be identified to species. This requirement forces the researches to make rapid, often incorrect decisions. A careful definition of study goals would leave both ecologists and polychaetologists happier and the few polychaetologists working full time on polychaete taxonomy less overwhelmed.

There is little support for all the other kinds of studies needed to describe and study polychaetes adequately. The result is that most of the polychaetologists are limping along, without being able to do even the necessary revisory work, and certainly without being able to apply theory or attempt to add truly new information to our descriptions of polychaetes. A rather sad conclusion, but I believe one in which experts on other groups also would concur.

Acknowledgments

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I would like thank the committee, Drs. M. Patricia Morse, Joan Ferraris and Jon Norenburg for giving me the opportunity to give the lecture. Dr. Leonard P. Hirsch read and rejected several versions of the paper, for which I am now very grateful; what makes sense in this paper is due to my friends; what appears hare-brained is my own responsibility.

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A NEW SPECIES OF *EUCHONE* (POLYCHAETA: SABELLIDAE) FROM THE NORTHWEST ATLANTIC WITH COMMENTS ON ONTOGENETIC VARIABILITY

R. Eugene Ruff and Betsy Brown

Abstract.—*Euchone bansei,* a new species of the polychaete family Sabellidae, is described from the continental slope and rise between Cape Cod, Massachusetts, and Cape Lookout, North Carolina. Juvenile and adult specimens are examined and ontogenetic variability is discussed. It is demonstrated that the number of abdominal depression setigers, the shape of the collar, and the number of radioles are not valid diagnostic characters for the identification of juveniles.

In response to interest in offshore oil and gas development, the Minerals Management Service (MMS) of the U.S. Department of the Interior sponsored research on benthic communities on the continental slope and rise (500–3000 m) off the eastern United States in three regions: (1) the U.S. North Atlantic near Georges Bank off Massachusetts, (2) the U.S. Mid-Atlantic off New Jersey, and (3) the U.S. South Atlantic off the Carolinas. As is typical in marine soft-bottom environments (Knox 1977), the macrofaunal communities in these regions are dominated by polychaetous annelids (Maciolek et al. 1987a, b; Blake et al. 1987). Because of the numerous samples collected and the small sieve mesh (300 μm) used throughout this sampling program, juvenile growth stages of many polychaete species were routinely collected. This paper describes a new species of *Euchone* (Polychaeta: Sabellidae) collected between 1345–2495 m depth along the U.S. Atlantic coast and examines some of the ontogenetic variability exhibited by this species.

Euchone bansei, new species
Figs. 1, 2

Euchone spp. Hartman & Fauchald, 1971: 179 [partim].

Euchone sp. 3. Maciolek et al., 1987a, b.—Blake et al., 1987.

Material examined.—off Martha's Vineyard, 4 May 1966, *Chain* station Ch 103, 39°43.6'N, 70°37.4'W, 2022 m, 8 specimens; 7 Sep 1963, *Atlantis* station A 58, 38°34.3'N, 72°55.0'W, 2000 ± 75 m, 3 specimens; near Baltimore Canyon, 19 May 1985, cruise MID-4 station 13-2, 37°53.29'N, 73°45.30'W, 1607 m, clayey mud, Holotype (USNM 115738); 19 May 1985, cruise MID-4 station 10-3, 37°51.73'N, 73°20.01'W, 2095 m, silty mud, 5 paratypes (USNM 115739); 16 Nov 1985, cruise MID-6 station 10-1, 37°51.77'N, 73°20.01'W, 2104 m, silty mud, 9 paratypes (BMNH ZB 1987.620–628); near Lindenkoehl Canyon, 16 May 1985, cruise MID-4 station 3-2, 38°36.75'N, 72°51.57'W, 2055 m, silty mud, 6 paratypes (BMNH ZB 1987.629–634); 17 May 1985, cruise MID-4 station 3-3, 38°36.75'N, 72°51.60'W, 2052 m, silty mud, 9 paratypes (USNM 115740); 17 May 1985, cruise MID-4 station 11-1, 38°40.10'N, 72°56.43'W, 1510 m, clayey mud, 22 paratypes (USNM 115741); 7 Aug 1985, cruise MID-5 station 12-2, 38°29.25'N, 72°42.22'W, 2495 m, sandy mud, 3 paratypes (USNM 115742); off Cape Cod, 25 Jul 1986, cruise NOR-6 station

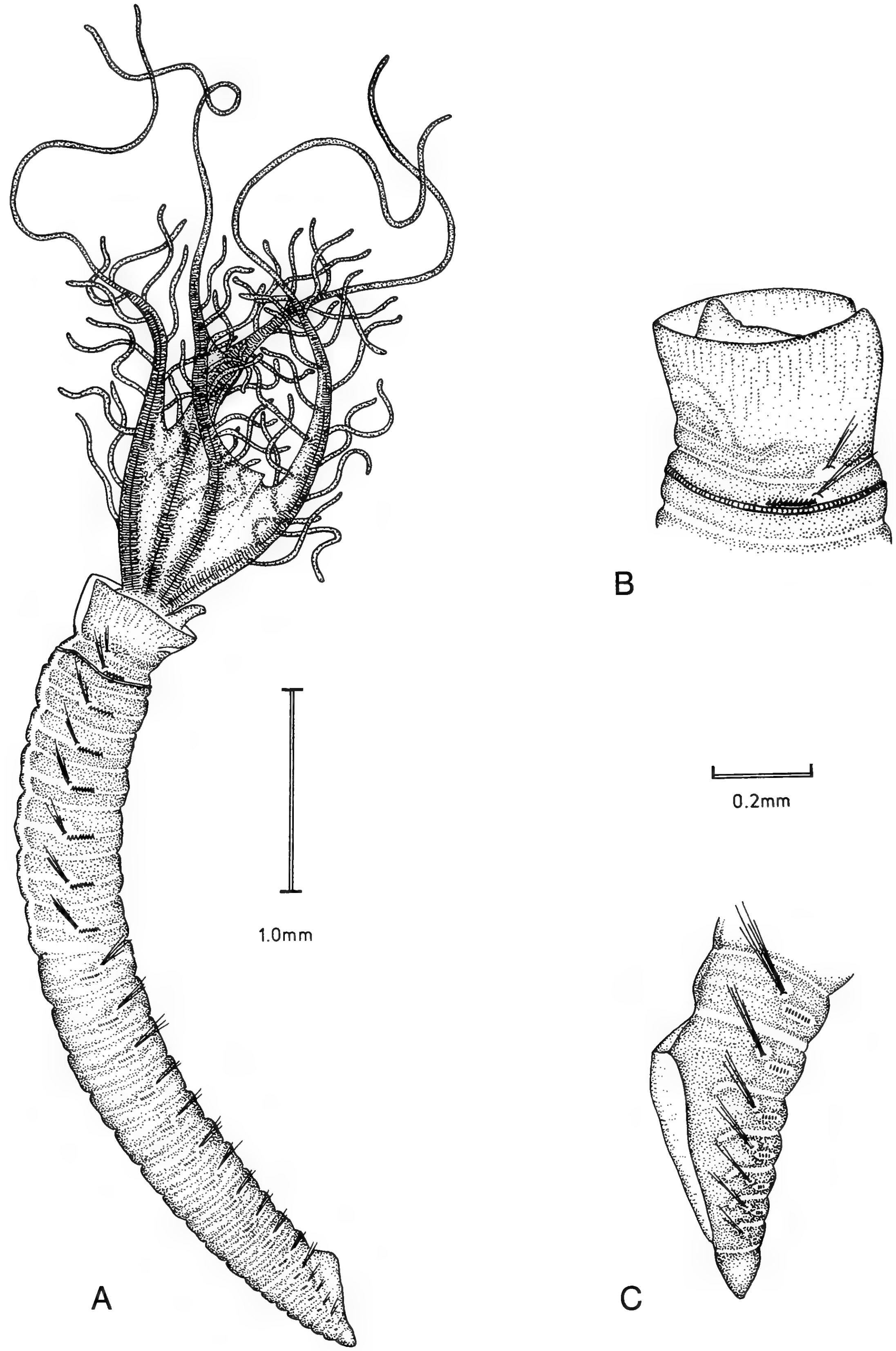

Fig. 1. *Euchone bansei* (holotype, USNM 115738): A, Entire animal in lateral view showing the right half of branchial crown; B, Collar and anterior region with branchiae not illustrated; C, Posterior region showing the anal furrow.

3-1, 41°01.55′N, 66°20.12′W, 1345 m, silty mud, 1 paratype (USNM 115743); near Lydonia Canyon, 29 Apr 1985, cruise NOR-2 station 6-2, 40°05.03′N, 67°29.13′W, 2108 m, sandy mud, 9 paratypes (USNM 115744); off Cape Lookout, 23 May 1985, cruise SA-4 station 4-3, 34°11.29′N, 75°38.67′W, 2015 m, silty mud, 2 paratypes (USNM 115745).

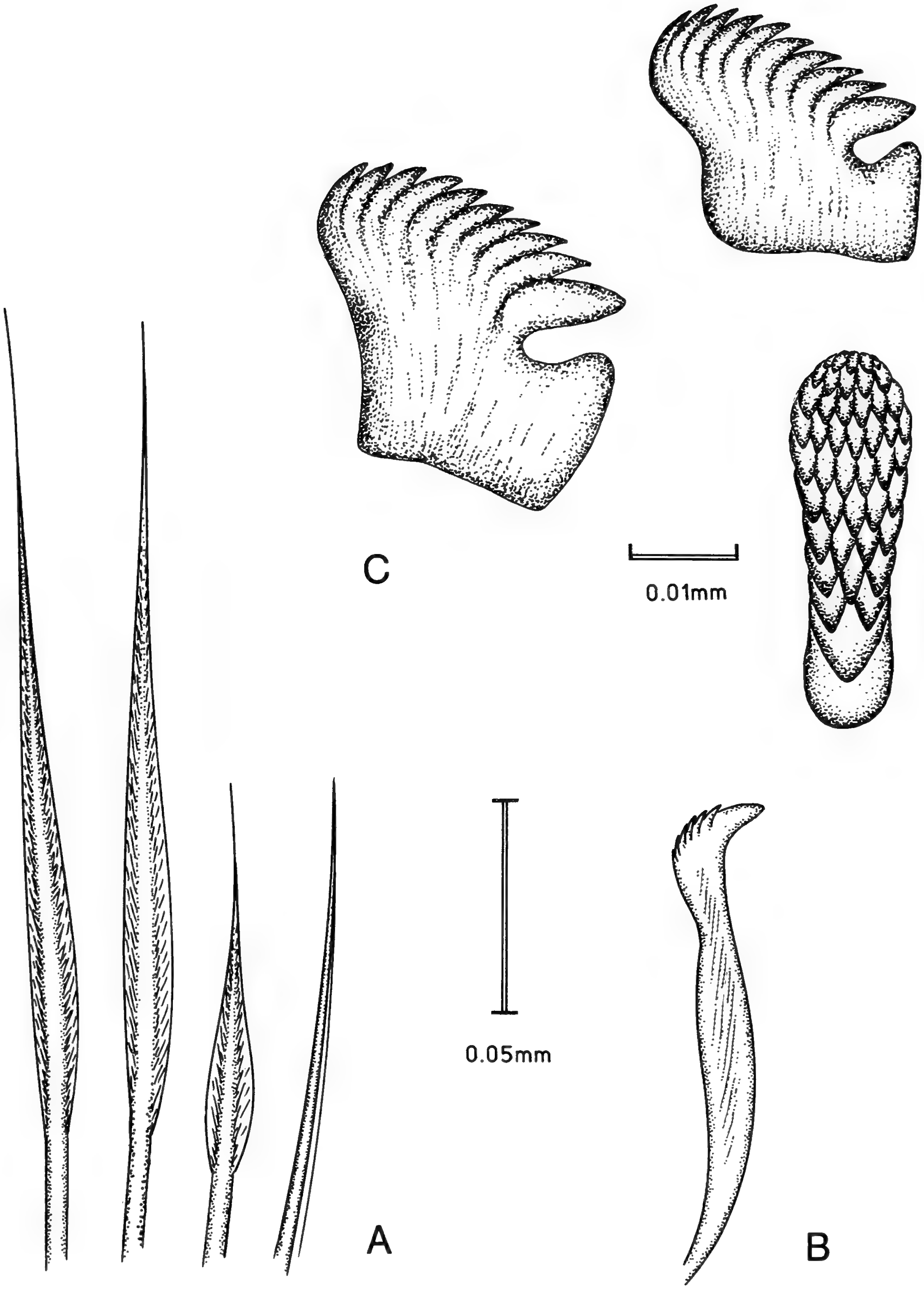

Fig. 2. *Euchone bansei* (paratype, BMNH ZB 1987.620): A, Thoracic notosetae from setiger three, including long and short limbate setae and a narrowly limbate bayonet seta; B, Thoracic neuroseta from setiger three; C, Uncini from abdominal setiger four in profile and in frontal view.

Diagnosis.—Small *Euchone* species with 17 abdominal setigers, last 6 associated with anal depression. Branchial crown with 4 pairs of radioles united with palmate membrane for half their length; radioles with long, filiform, pinnule-free ends. Collar entire laterally and ventrally, separated by mid-dorsal gap, of even height all around, extending to branchial basis. Ventral shields absent. Thoracic notopodia with long and short limbate setae and pointed bayonet setae. Abdominal uncini with quadrate base, small main fang, and crest of numerous smaller teeth.

Description.—Adult holotype 4.0 mm in length (excluding radioles), 0.5 mm in width along posterior thorax (Fig. 1A). Other adult specimens 2.2–5.9 mm in length, 0.3–0.8 mm in width; branchial crown contributing additional 4.4 mm in largest individuals. Four pairs of radioles connected for half their length by delicate palmate membrane; each radiole with about 20 subequal pinnules alternating along axis and a pinnule-free filiform tip contributing up to half of total radiole length. Dorsal lips with elongate-triangular radiolar appendages, about one-half pinnule length, densely ciliated; pinnular appendages not observed. Paired ventral lips shorter, rounded.

Peristomium produced into triangular projection ventral to radioles. Collar entire ventrally and of nearly equal height laterally and ventrally in adult (Fig. 1B), reaching approximately to base of branchiae; dorsal gap very narrow; otocysts not observed. First setiger one-half length and narrower than following thoracic setigers. Thin postsetal glandular girdle encircling second setiger. Ventral shields absent.

Abdomen with 17 setigers, last 6 associated with anal depression; wings of depression flaring, connected anteriorly by thin membrane (Fig. 1C). Pygidium triangular, slightly longer than wide.

First setiger with single bundle of long, narrow limbate setae and shorter bayonet setae; other thoracic notosetae of three kinds: superior arc of long limbate setae, and inferior group of short limbate setae and slender pointed bayonet setae with narrow wings (Fig. 2A). Thoracic neuropodia with about 12 long-handled acicular uncini in each fascicle (Fig. 2B). Abdominal notopodial tori with 10–17 uncini, each with quadrate base and small main fang surmounted by numerous rows of smaller teeth (Fig. 2C); shape of uncini nearly constant within each torus, but main fang progressively smaller in posterior setigers. Abdominal neuropodia with 3–4 narrowly limbate setae per fascicle.

Sexes separate with gametes occurring laterally between dorsal and ventral longitudinal muscle bundles in posterior thoracic and anterior abdominal segments. Eggs irregular in outline, up to 0.1 mm in diameter. Sperm short-headed, with blunt acrosomes, approximately 5 μm long excluding flagella.

Methyl green stain in 70 percent ethanol (Banse 1970) readily accepted both dorsally and ventrally on most of body including pygidium and wings of anal depression. Staining cells absent in radioles, at anterior margin of collar, in glandular girdle, in intersegmental furrows, along fecal groove, around parapodia, and in narrow band of cells encircling each segment at level of setae.

Distribution.—*Euchone bansei* is found from the southern flank of Georges Bank off Cape Cod, Massachusetts, southward to Cape Lookout, North Carolina. The species occurs in sandy to clayey muds in depths of 1345–2495 m and is found most often at about 2000 m in abundances occasionally exceeding 100/m^2.

Etymology.—This species is named in honor of Dr. Karl Banse in recognition of his significant contributions to the knowledge and taxonomy of the Sabellidae.

Ontogenetic Variability

The routine use of 300-μm mesh sieves throughout the MMS sampling program resulted in the collection of a large number of sub-adult and juvenile specimens of *Euchone bansei.* After selection of the type material, an additional 185 specimens from across the sampling region were examined in detail. Ocular micrometer measurements were made on the total length from the top of the collar to the tip of the pygidium and on the width of the last thoracic setiger. Counts were made on the number of thoracic and abdominal setigers, on the number

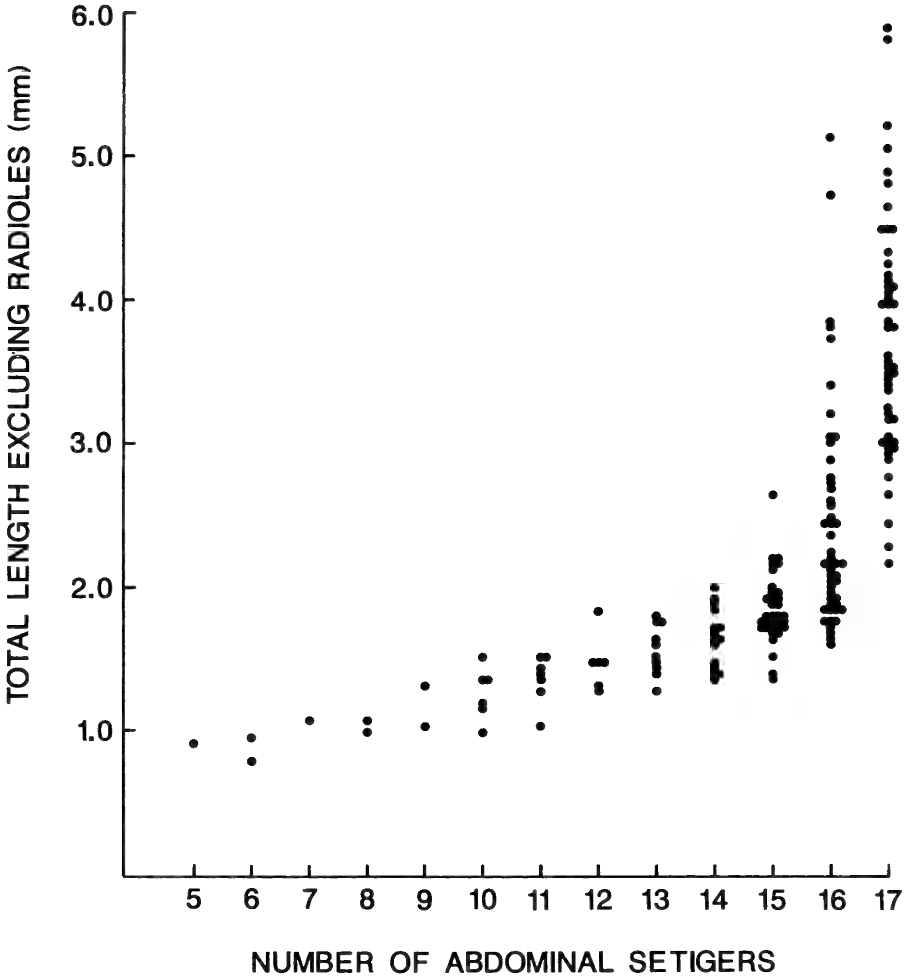

Fig. 3. Relationship between number of abdominal setigers and total body length (excluding radioles) for 185 specimens of *Euchone bansei.*

of segments in the anal depression, and on the number of radioles. Observations were made on the shape and height of the collar.

The smallest individuals retained by the sieves are less than 1.0 mm in length and about 0.1 mm wide. At this size, all thoracic setigers and five or more abdominal setigers are present. The first segment in the anal depression usually appears as abdominal setiger 12, but in three of the 185 specimens measured it appears as abdominal setiger 11. Depression segments are added through abdominal setiger 17. No specimens were found with more than six depression segments or 17 total abdominal setigers. In the three cases where the anal depression begins at setiger 11, the total abdominal setiger count is 16.

There is a statistically significant correlation between total body length and the width of the posterior thoracic segment ($r^2 = 0.79$, $P < 0.005$), revealing that *E. bansei* exhibits a very constant pattern of growth throughout its life. When total length is plotted as a function of the number of abdominal setigers, it is evident that most growth is accomplished after the majority of the segments are in place (Fig. 3). Sexual maturity is attained after the individual has grown considerably in total size and added most or all of the setigers. Gametes are found only in a few of the largest specimens having 16 abdominal setigers, and in many of the larger individuals having 17 abdominal setigers.

The height and shape of the collar depends on the size of the specimen. In the smallest individuals it is short, oblique, and

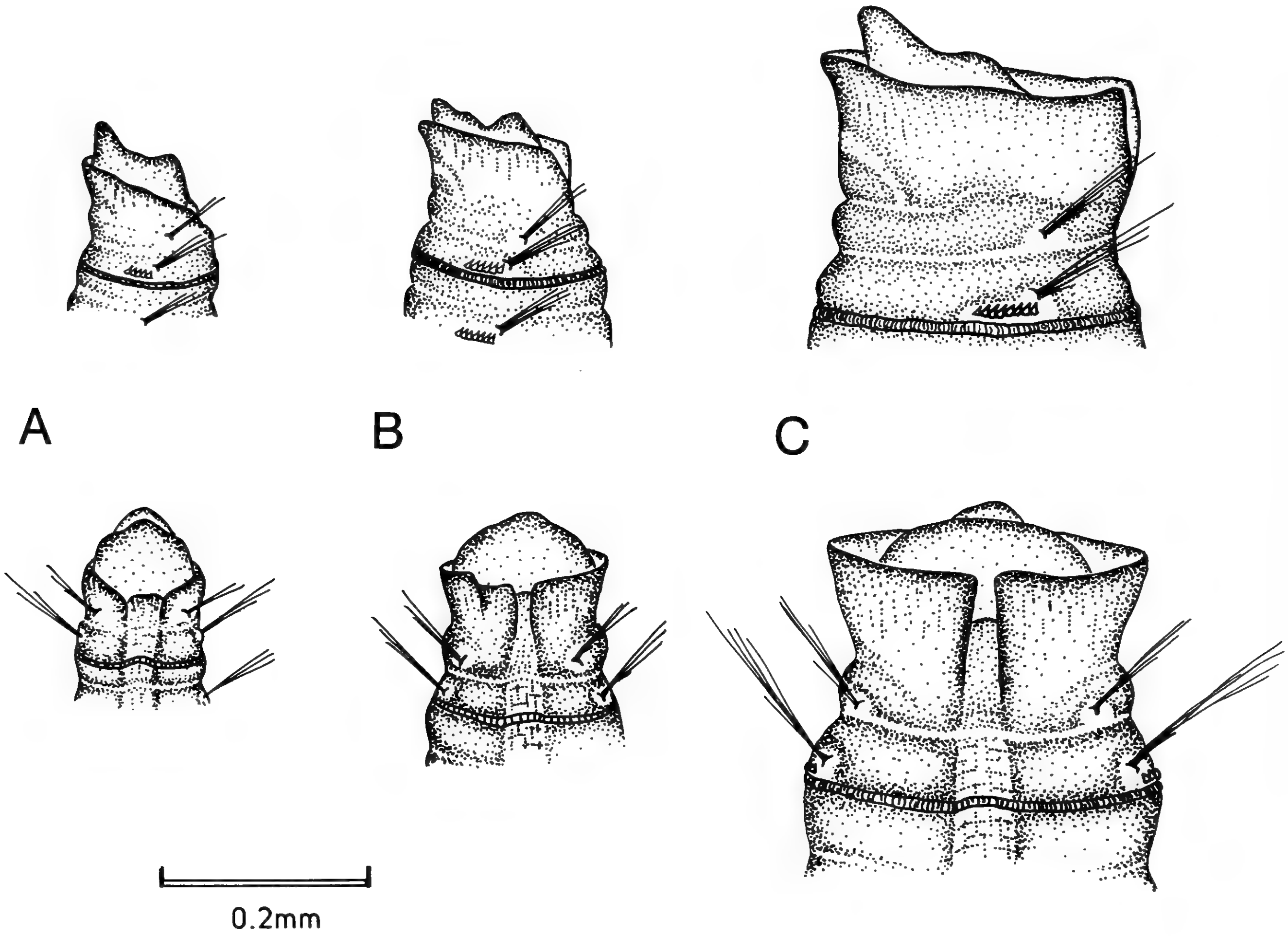

Fig. 4. Collar development in juvenile specimens of *Euchone bansei* in lateral and dorsal view: A, Six abdominal setiger stage; B, Twelve abdominal setiger stage; C, Sixteen abdominal setiger stage.

relatively undeveloped on the dorsal side, wrapping closely against the anterior body (Fig. 4A). The collar lengthens dorsally and laterally, becoming more foliaceous as the worm adds abdominal setigers (Fig. 4B, C). By the time the specimen has become sexually mature the collar extends to the base of the branchiae and is of nearly equal height all around (Fig. 1B).

Only two pairs of radioles are present on the smallest specimens examined. However, even at this stage the branchiae have the long filiform free ends characteristic of the adults. By the time the abdomen has

Table 1.—Comparison of small species of *Euchone*: (1) Pre-depression setigers in the abdomen; (2) Abdominal depression setigers in adult specimens; (3) Pairs of radioles; (4) Length:width ratio of the blades of the inferior series of limbate thoracic notosetae; (5) Occurrence of ventral shields; (6) Ratio of the length of the free tips of the radioles relative to the total length of the radioles. Information is derived from the original descriptions and from Banse (1970).

Species	1	2	3	4	5	6
Euchone arenae Hartman, 1966	6–9	6	5–7	4:1	Present	1:6
Euchone elegans Verrill, 1873	12–15	8–10	6–8	5:1	Present	1:6
Euchone hancocki Banse, 1970	5	3	4	10:1	Absent	1:3
Euchone incolor Hartman, 1965	6	3	3	5:1	Absent	1:4
Euchone rosea Langerhans, 1884	10–12	5–7	5–8	6:1	Present	1:10
Euchone bansei New species	11	6	4	9:1	Absent	1:2

added the tenth setiger, a third pair of radioles is developing ventral to the first two pairs. The fourth and final pair appears about the time the fifteenth abdominal setiger is developing.

Discussion

Euchone bansei is most similar to *E. rosea* Langerhans, 1884, from the eastern Atlantic off Europe and North Africa (Table 1), but it differs in lacking distinct ventral shields and in having fewer radioles, each with long rather than short filiform tips. *Euchone bansei* shares several characters with *E. hancocki* Banse, 1970, including four pairs of radioles with long free ends, a short and narrow first thoracic setiger, an inferior group of thoracic notosetae with narrow wings, and the absence of ventral shields. *Euchone bansei,* however, has a total of 17 abdominal setigers instead of eight as in *E. hancocki,* and it lacks a girdle of glands on the first abdominal setiger.

No seasonality could be detected in the growth stages of this species throughout the year. Sexually mature adults, juveniles with no depression setigers, and all intermediate stages were found in samples taken in the spring, summer, and winter months.

As noted by Banse (1970) for other small species of *Euchone,* all of the pre-depression setigers are in place before the first depression setiger is formed. Sub-adult specimens have fewer depression setigers, and the smallest individuals entirely lack the depression, negating the utility of this character for the specific determination of juvenile specimens. Ontogenetic differences between the juveniles and adults of *E. bansei* also occur in the shape of the collar and the number of branchial radioles. These traditional diagnostic characters, therefore, can be considered only when dealing with adults of the species of *Euchone.*

Several other characters, however, remain constant as the specimens grow. The inferior series of thoracic notosetae have narrow wings rather than being broadened, an unusual feature within the genus which is helpful in confirming the identity of small *Euchone bansei.* The elongated free ends of the radioles, present during all observed stages of growth, is another useful character. Staining with methyl green also affords a high degree of accuracy in distinguishing this species from other small sabellids occurring in the same sample. The juveniles have fewer stain-accepting cells per unit area than the adults, and some variability in the distribution of individual gland cells is evident. However, the lack of stain-accepting cells in the intersegmental furrows and at the level of the parapodia results in a distinctly biannulate appearance to each setiger, and the pattern and uniform intensity of the staining regions when viewed in total are distinctive.

Acknowledgments

We wish to thank Drs. James A. Blake, Nancy Maciolek, Brigitte Hilbig, and two anonymous reviewers for valuable discussions and for critically reviewing the manuscript. Ms. Jennifer Taylor brought the excellent holotype to our attention, and Ms. Barbara Greene assisted with typing and production of the manuscript. This work was partially supported by Contract No. 14-12-0001-30064 from the U.S. Department of the Interior, Minerals Management Service, to Battelle Memorial Institute.

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PARALVINELLA HESSLERI, NEW SPECIES OF ALVINELLIDAE (POLYCHAETA) FROM THE MARIANA BACK-ARC BASIN HYDROTHERMAL VENTS

Daniel Desbruyères and Lucien Laubier

Abstract.—A new alvinellid polychaete, *Paralvinella hessleri,* from the Mariana back-arc basin hydrothermal area is described. It is morphologically close to *P. bactericola, P. palmiformis* and *P. grasslei,* from active vents in the eastern Pacific. Biogeographical implications are discussed herein.

The first alvinellid polychaete, *Alvinella pompejana,* was collected by D.S.R.V. *Alvin* from honeycomb-like structures on the chimney walls of active hot vents at 21°N Eastern Pacific Rise hydrothermal site (Desbruyères & Laubier 1980). Since that time, specimens collected on American, French and Canadian submersible dives on the east Pacific ridges have expanded our knowledge of alvinellids. These worms until now have been exclusively sampled associated with warm and hot deep-sea vents in the eastern Pacific ridge system. Six species and one sub-species, belonging to two genera, have been described from the East Pacific Rise, Galápagos Ridge, Guaymas Basin, Explorer and Juan de Fuca Ridges (Desbruyères & Laubier 1982, 1986, 1989). The examination of all these taxa led us recently (1986) to propose the erection of a new family Alvinellidae, which seems to be primitive within the order Terebellida.

Recently, an *Alvin* study of the Mariana Back-Arc Basin resulted in the discovery of two large vent areas at 3600–3700 m. The vent fields lie on the flank of active axial volcanoes (Craig et al. 1987) with a striking hydrothermal fauna. According to Hessler et al. (1987), patterns of faunal distribution at the vents are similar to those seen on the East Pacific Rise although the dominant organisms belong to different and new taxa.

The alvinellid species described here were sent to us by R. R. Hessler of the Scripps Institution of Oceanography. The specimens were collected by submersible *Alvin* on the rocks directly exposed to venting water whose temperature was recorded up to 25°C.

Order: Terebellida
Family: Alvinellidae Desbruyères & Laubier, 1986
Paralvinella hessleri, new species

Type locality, material examined.—Thirty three specimens collected during *Alvin* dives 1831 (04/16/87) at Illium vent site (depth 3595 m, 18°12.8′N and 144°42.4′E), 1843 (05/04/87) and 1845 (05/06/87) at Alice Springs (depth 3640 m, 18°12.6′N and 144°42.4′E). Holotype (dive 1831) deposited in the collections of the Division of Worms, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 119431). Paratypes (number 5) from the same dive deposited in the collections of the "Laboratoire des Vers," Muséum national d'Histoire naturelle de Paris (UC 90/A 908).

Etymology.—This species is named for Dr. Robert R. Hessler, Scripps Institution of Oceanography, leader of the biological study of the Mariana vents.

Description.—Holotype 22 mm in length and 2.1 mm in greatest width with 60 setigerous segments (Fig. 1A). Paratypes range from 52 to 61 setigerous segments with the majority having 58 to 61. Color pinkish after preservation in ethanol, with capillary setae yellow, modified setae brown. Body gradually tapering from about setigerous segment 30 to the end of the body. Ventral shields in the anterior third.

Prostomium medially reduced with a median incision and two well developed lateral lobes ventrally enclosing peristomium (Fig. 2A). Buccal apparatus complex, comprising a ventral globular bulky organ (a), two lateral, large and strong pointed tentacles (b) bearing a deep groove without ciliation, and many grooved and ciliated smaller tentacles (c) inserted in two groups on a quadrilobed upper lip (Fig. 3A). The whole apparatus or each part (e.g. ciliated tentacles, large tentacles and globular organ) eversible.

First segments (II and III) achaetous and fused to the first three setigerous; these five segments are not discernible ventrally. The first 15 to 20 setigerous segments with notopodia only.

First three notopodia smaller than others and dorsally elevated. Branchial region formed by segments III to VI (an achaetous segment plus three setigerous segments). Branchiae four pairs, all similar, strong and regularly attenuated, and arranged in two adjacent groups. Branchial stem with large number of slender filaments inserted on two opposite narrow areas; branchial filaments cylindrical with small secondary filaments arising on two opposite lines. Setiger 4 (segment VII) with a median dorsal expansion which protrudes forward (Fig. 1B).

Notopodia, from setiger 4 to 13–17 (7 excepted), cylindrical with a dorsal digitiform lobe (Fig. 3C) bearing two groups of capillary setae, one with short and the other with long. Setigerous segment 7 strongly modified, lacking cylindrical notopodia but bearing, on each side, 4 to 5 very large acicular notopodial hooks directed posteriorly. Setigerous segment 8 with cylindrical notopodium and very strong digitiform lobe directed forward (Fig. 2B and 3C).

Cylindrical notopodia and uncinigerous neuropodial tori on each segment from segment 15–20, both to end of body. Uncini numerous (20 to 50 per torus) in single rows, with teeth facing anteriorly (retrogressive situation). Uncini with one main tooth surmounted by one smaller secondary tooth (Fig. 3B) as in all other alvinellids. Pygidium rounded with inconspicuous papillations.

Tubes whitish and corneous in aspect, amoeba-like in shape with long anchor filaments (Fig. 2D). Tube walls thick and multilayered. Inner surface bearing huge filamentous bacterial mats.

Ecology.—All the specimens have been found in tubes on rocks directly exposed to venting water whose temperature was recorded up to 25°C. The holotype was collected inside Illium vent site from Whelk's Club hot vent area near a hot smoker whose temperature is 282°C.

Discussion

Since the discovery of the first Alvinellinae, another genus, five species and one sub-species have been described, all sampled from active hydrothermal vent areas of the eastern Pacific; a new family was erected within the order Terebellida (see Desbruyères & Laubier 1986, Holthe 1986) to accomodate these unusual polychaetes.

Specimens collected from the Mariana Back-Arc Basin hydrothermal vents undoubtedly belong to *Paralvinella* and are morphologically close to *Paralvinella grasslei* Desbruyères & Laubier, 1982, *P. palmiformis* Desbruyères & Laubier, 1986, and *P. bactericola* Desbruyères & Laubier, 1989. All share the following features: prostomium medially reduced with two lateral expansions, four pairs of bipinnate branchiae with secondary slender filaments in opposite arrangement, uncini present posterior to the modified segment and buccal organ complex with large paired, grooved non-cil-

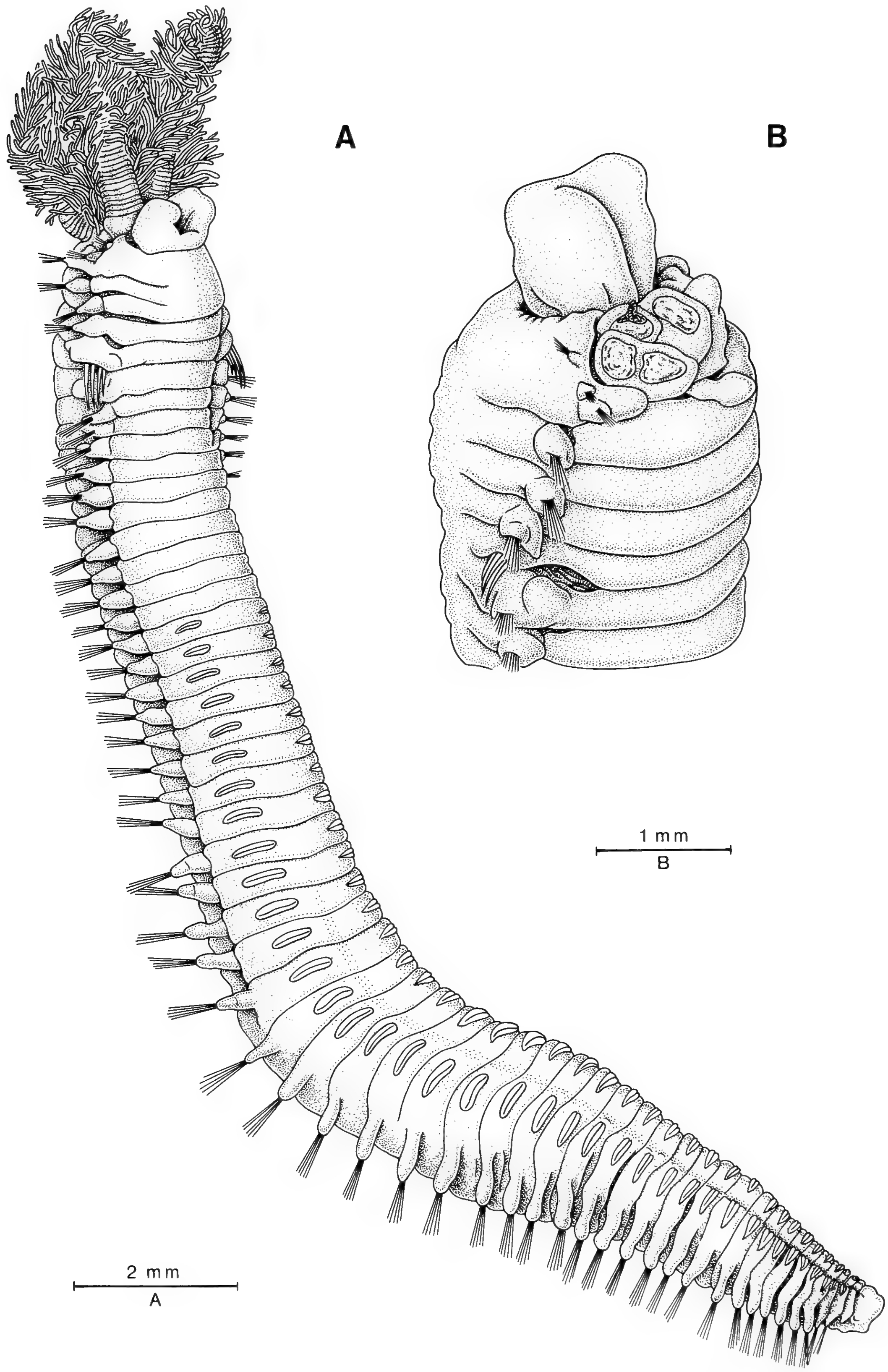

Fig. 1. *Paralvinella hessleri*: A, Habitus in latero-ventral view. Buccal apparatus invaginated; B, Anterior end in dorso-lateral view, branchiae removed.

iated tentacles. *Paralvinella hessleri* differs from these three species by the shape of the buccal structures, the first appearance of the uncinigerous tori, the presence of a stouter notopodial lobe on setiger 8 and the fusion of the first five segments as in *Alvinella* spp. (Figs. 2B and 4).

Paralvinella grasslei and *P. palmiformis* are closely related, while *P. bactericola* differs from both by the structure of its buccal

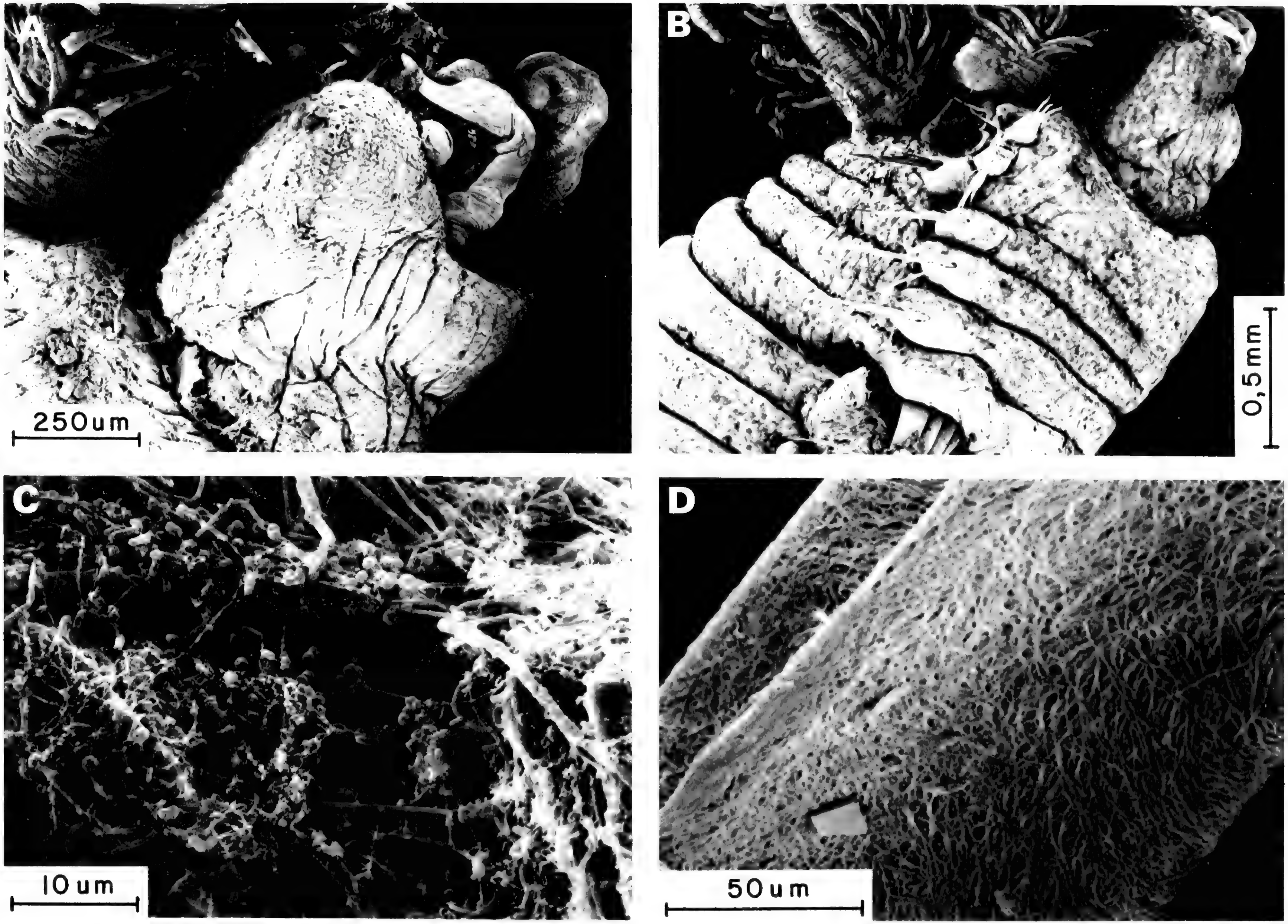

Fig. 2. *Paralvinella hessleri,* scanning electron photomicrographs: A, Lateral lobes of the prostomium enclosing, ventrally, the peristomium, (right side, lateral view); B, Branchial fused segments in right side lateral view; C, Bacterial mats on the inner part of the tube; D, Anchor filaments of the tube.

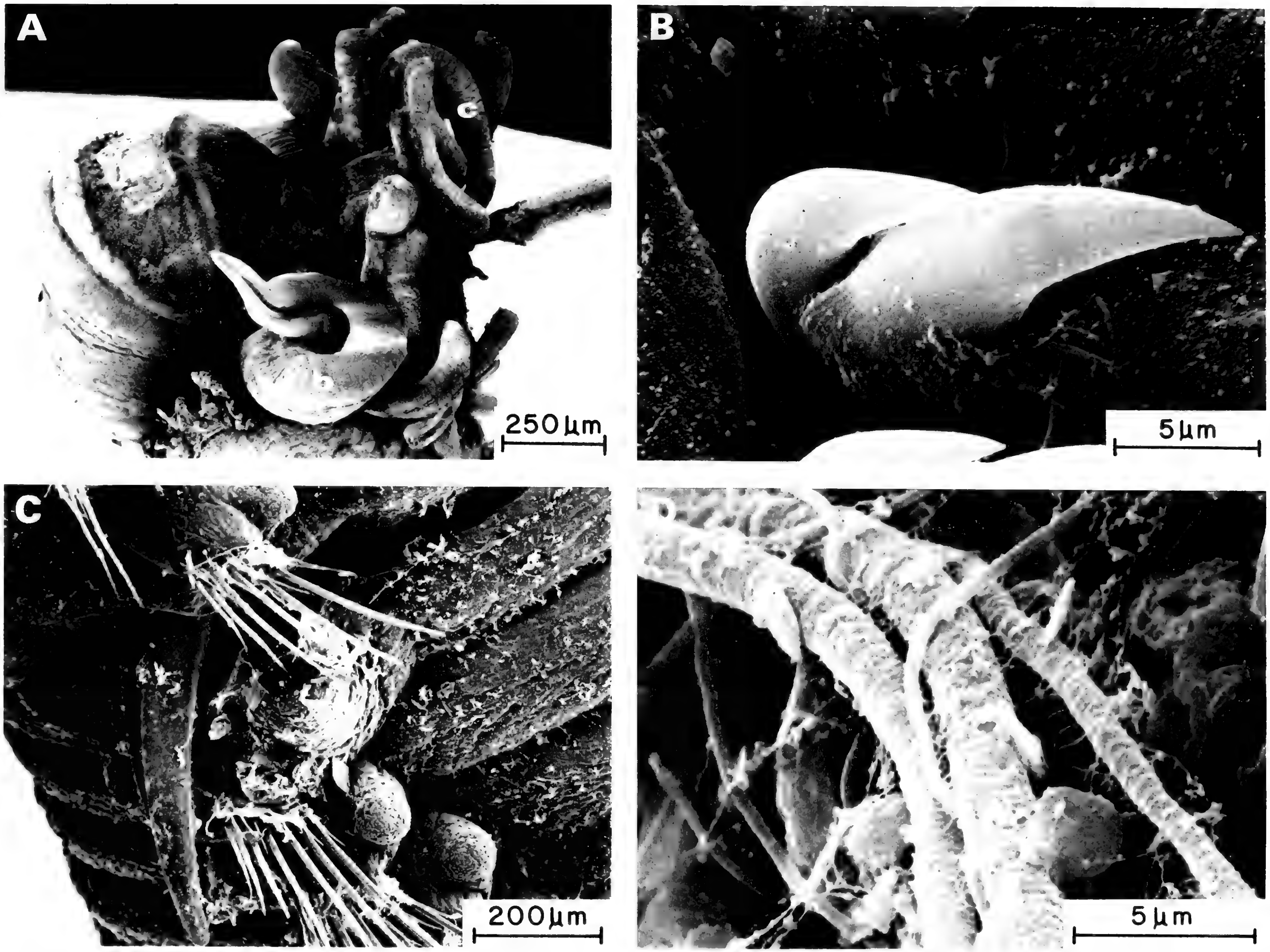

Fig. 3. *Paralvinella hessleri,* scanning electron photomicrographs: A, left side lateral view of the everted buccal apparatus, (a) ventral organ, (b) lateral paired tentacles, (c) buccal grooved tentacles; B, Uncinus of a median setigerous segment; C, Left side latero-dorsal view of the left transformed notopodium (seventh setigerous segment); D, Filamentous bacteria from the inner part of the tube.

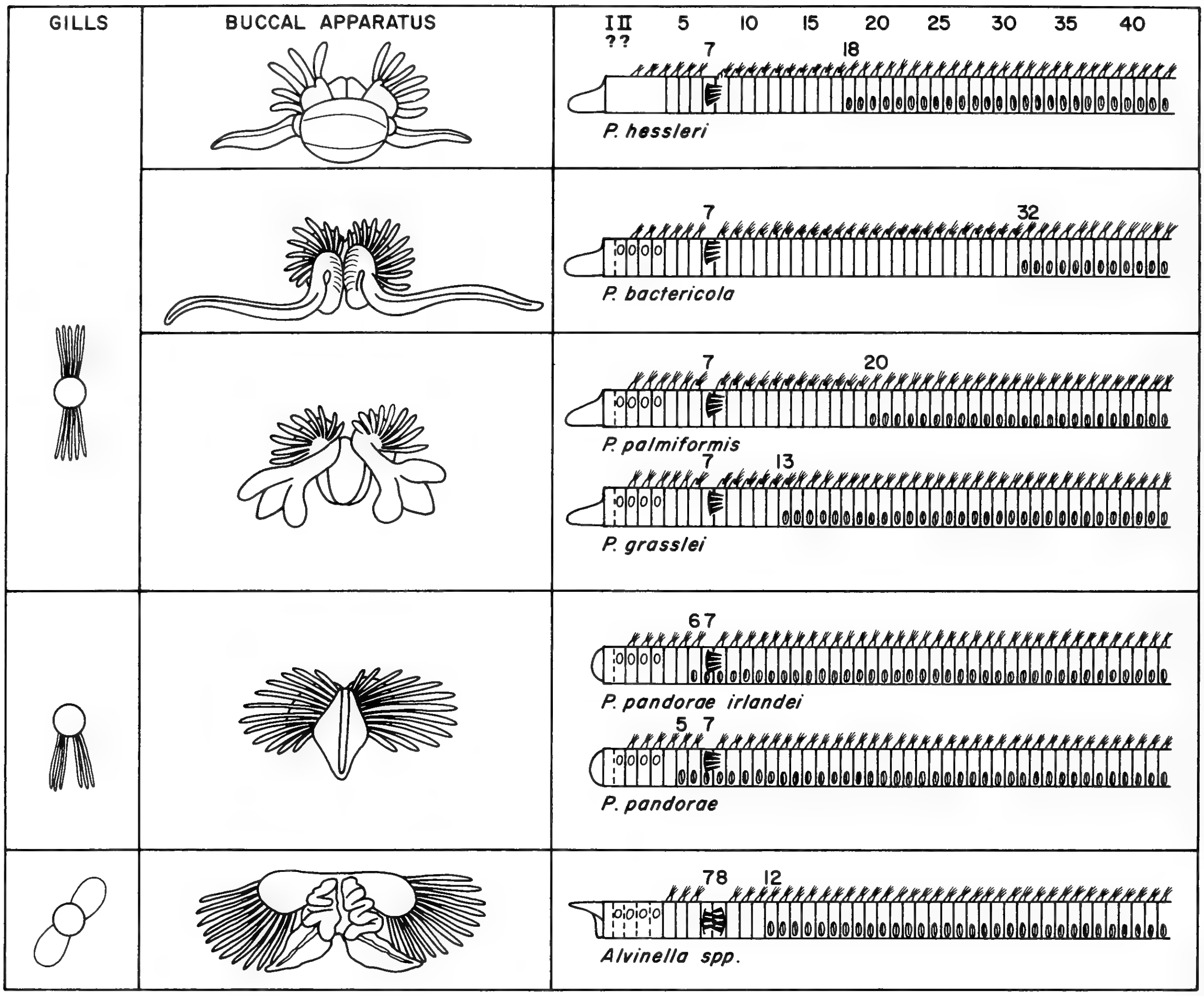

Fig. 4. Distinctive characters of the seven species and subspecies of Alvinellidae.

apparatus and the posterior position of the neuropodia. Due to its buccal apparatus with two large and strong pointed tentacles, *P. hessleri* has close relationship with *P. bactericola.* On the contrary, the pair of sibling species *P. grasslei* and *P. palmiformis* is characterized by two buccal structures ending in three rounded lobes. The ventral globular bulky organ of *P. hessleri* resembles the ventral lobe of *P. grasslei* and *P. palmiformis.* Still, its absence in *P. bactericola* is not definitely established due to the small size of the sample and the possibility of invagination. The first neuropodium of *P. hessleri* (setigerous segment 18) appears in an intermediate position between *P. grasslei* (setigerous segment 13) and *P. palmiformis* (setigerous segment 20). In *P. hessleri,* the fusion of anterior segments and the tendency towards reduction and constancy in number of segments can be considered as apomorphous conditions within Alvinellidae. At present, we can consider *P. hessleri* as a "recent" species within the genus; it exhibits clear relationship with the group *P. bactericola* and *P. grasslei* and *P. palmiformis.*

The morphological likeness between *P. bactericola* and *P. hessleri* led us to assume a common ancestor. The Mariana Back-Arc Basin is located about 5000 nautical miles west from the eastern Pacific ridge system where all other *Paralvinella* have been found. This young back-arc basin, probably less than 10 million years old, has no physical connection with the mid-oceanic ridge system and is strongly isolated. Such habitat isolation, combined with close relationship between *P. hessleri* and *P. bactericola,* led us to assume 1) the existence of very efficient dispersal mechanisms, or 2) the possibility that submarine volcanoes or organic matter patches could act as stepping stones for *Paralvinella* dispersal. The youngest stage of *Paralvinella,* presently known, is a twelve-segmented erpochaeta of *P. pandorae irlandei* (Desbruyères & Laubier 1986). By comparison with a few examples of ampharetid species, we recently concluded that alvinellids should probably have a short larval life (Desbruyères & Laubier 1986), while the opposite hypothesis could be supported by comparison with several terebellids. The hypothesis of submarine volcanoes acting as stepping stones for the dispersal of benthic species is supported by recent results on branchiate polynoids (Desbruyères & Laubier 1988). Concerning the two sibling species *P. palmiformis* and *P. grasslei,* it is though that they arise from a common ancestor by allopatric speciation after the original area was separated into two distinct hydrothermal districts, north and south of the Oregon subduction zone some 26 million years ago by the overlapping American plate (Tunnicliffe 1988). At the opposite *P. bactericola* and *P. grasslei* dwell close together in Guaymas Basin, demonstrating a strong sympatric speciation: the first associated with bacterial mats, the second with vestimentiferans and sulfides.

Acknowledgments

We wish to thank R. R. Hessler of the Scripps Oceanographic Institution for the material on which this study is based as well as scientists and crew members of the Mariana Back-Arc Basin expedition. We thank, too, M. A. Boudrias for his help and the chief scientist of the first leg H. Craig.

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A NEW SPECIES OF *ODONTOSYLLIS* (POLYCHAETA: SYLLIDAE) FROM TWIN CAYS, BELIZE

David E. Russell

Abstract.—*Odontosyllis twincayensis* is illustrated and described from Twin Cays, a mangrove island located on the Belizean barrier reef. The species is distinguished by setal blade shape and a unique combination of features that includes a distinct occipital flap, a trepan with 6 teeth, a large bulbous proventricle with 35 to 44 muscle cell rows, and bidentate setal blades of only one type.

An investigation of the distribution of syllid polychaetes in mangrove and adjacent shallow-water habitats at Twin Cays, Belize, revealed a multitude of species (Russell 1987). Forty-three syllid species were recorded from 24 benthic cores. Among the over 7800 specimens examined were two individuals of a new species of *Odontosyllis* described below.

The material examined has been deposited in the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.

The generic definition is that of San Martín (1984).

Odontosyllis Claparède, 1863

Odontosyllis twincayensis, new species

Fig. 1

Material examined.—West Bay, Twin Cays, Belize, Caribbean Sea; 20 cm depth, rootmat of *Rhizophora mangle* covered with a dense growth of *Halimeda opuntia* f. *triloba*; Nov 1983: holotype, core H-8U (USNM 102372); paratype, core H-1U (USNM 102373).

Comparative material examined.—Hutchinson Island, Florida, North Atlantic; 11.8 m; May 1972: *Odontosyllis longigulata* Perkins, 1981; holotype (USNM 60445); 2 paratypes (USNM 60447). Off North Carolina, North Atlantic; 130 m; Apr 1965: *Odontosyllis longiseta* Day, 1973; holotype (USNM 43120); 25 paratypes (USNM 43121). Barceloneta, Puerto Rico, North Atlantic; 23 m; Sep 1974: *Odontosyllis longiseta,* 1 specimen (USNM 52255) id. by C. Long.

Description.—Body pale yellow without color markings, pharynx pale amber. Body more or less cylindrical anteriorly. Holotype a gravid female, 2.4 mm long, posteriorly incomplete, with 16 setigers, 0.7 mm wide across proventricle without parapodia. Paratype a mature male (?), 0.64 mm long, posteriorly incomplete, with 7 setigers, 0.20 mm wide across proventricle without parapodia. Body length, width, and number of setigers in complete specimens unknown.

Prostomium oval, about twice as long as wide, with two pairs of large garnet eyes each with several small lens-like elements, posterior pair slightly smaller and closer together than anterior pair (Fig. 1A). Paratype with third pair of smaller lensed eyes on anterior margin of prostomium; eyes of pair well separated, each immediately lateral to a lateral antenna. Antennae short, digitiform, similar in size; median antenna originating midway between anterior pair of eyes; lateral antennae arising from anterior margin of prostomium. Palps about as long as prostomium, directed ventrally, fused basally. Pair of C-shaped, ciliated nuchal

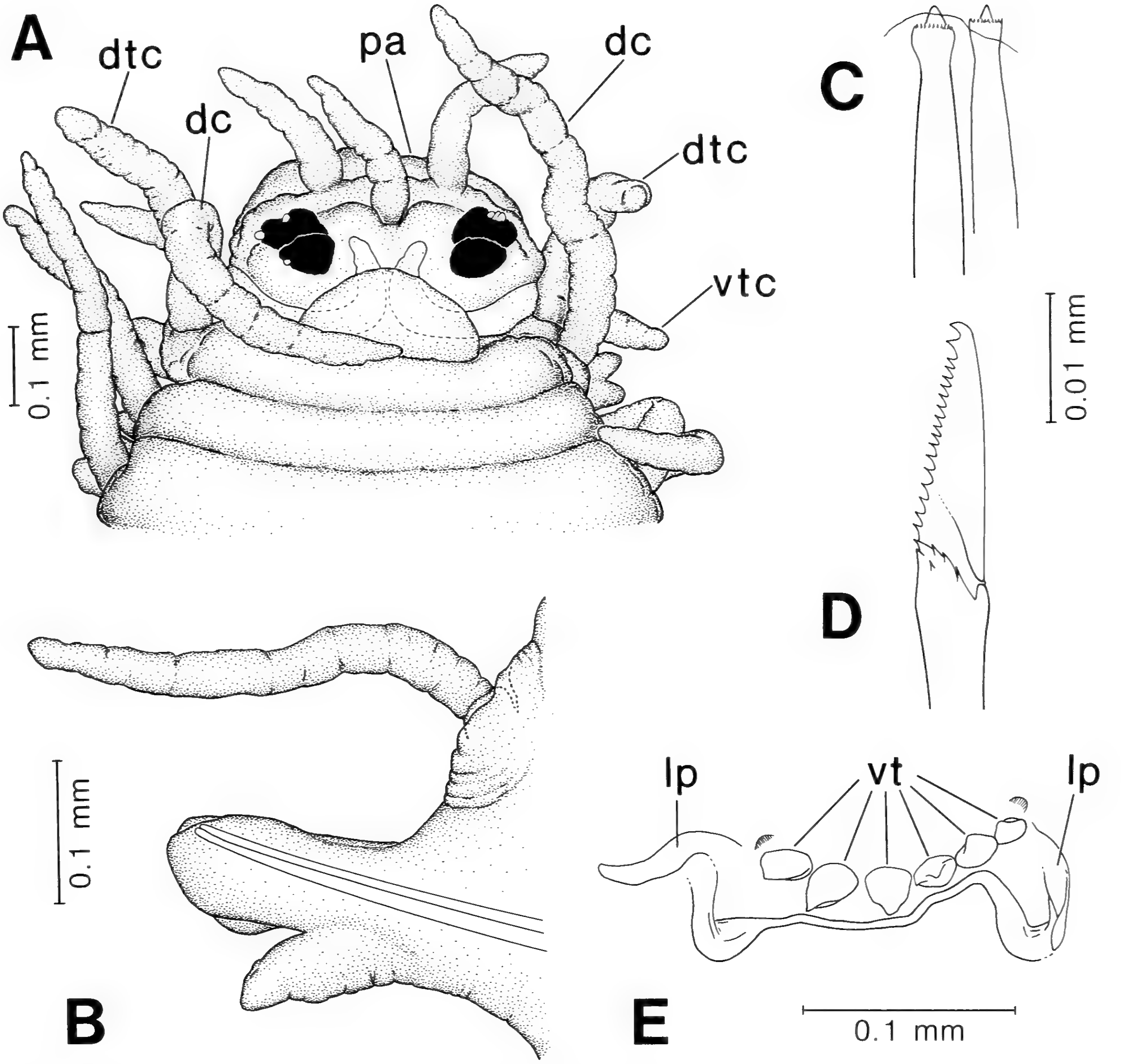

Fig. 1. *Odontosyllis twincayensis,* holotype (USNM 102372): A, Anterior end, dorsal view (slightly compressed dorsoventrally, prostomium and palps curving ventrally), setae omitted; B, Parapodium from setiger 13, posterior view, setae omitted; C, Aciculae from setiger 16; D, Inferior compound seta from setiger 16, scale same for C and D; E, Pharyngeal teeth and plates; dc = dorsal cirrus; dtc = dorsal tentacular cirrus; lp = lateral plate; pa = palp; vt = ventral teeth; vtc = ventral tentacular cirrus.

organs along posterior margin of prostomium, medial portion of each extending anteriorly, terminating between eyes; laterally, nuchal organs forming part of deep groove between prostomium and peristomium. Peristomium reduced dorsally, with clearly defined occipital flap extending anteriorly, partially covering nuchal organs. Two pairs of tentacular (peristomial) cirri, digitiform, smooth or with a few indistinct articulations; ventral tentacular cirri about as long as antennae, dorsal tentacular cirri about 1.5 times length of ventral tentacular cirri.

Parapodia divided distally into presetal and postsetal lobes (Fig. 1B). Two aciculae per parapodium in setigers 13 and 16, both dorsal to setal fascicle; each tapering distally to pointed tip with serrated subterminal expansion or rim (Fig. 1C). Dorsal cirri mostly smooth, or with a few partial, indistinct articulations most common distally (Fig. 1A, B); longest dorsal cirrus on setiger 1, thereafter dorsal cirri similar in length. Ventral cirri short, fusiform, partially fused to ventral surfaces of parapodia, not extending beyond tips of parapodia. Dorsal and ventral cirri of middle and posterior setigers, anal cirri, and pygidium unknown.

Simple setae not observed. Seventeen to 19 compound setae per parapodium in setigers 13 and 16; all blades on these parapodia similar in size and shape (Fig. 1D), approximately 19 μm long, maximum width about 4.4 μm, blade-length to blade-width ratio 4.0–4.4, bidentate with similar, small terminal and subterminal teeth. Blade cutting edge straight to slightly convex, bearing short, coarse serrations along entire length. Proximal oblique edge of blade not discernible near blade cutting edge. Shaft heads of compound setae all similar, slender, about 5.3 μm wide, bearing short serrations.

Pharynx extending to setiger 6, trepan with ventral row of 6 teeth and 2 lateral plates (Fig. 1E). Proventricle with about 44 narrow, indistinct muscle cell rows, occupying setigers 7 through 14, 0.98 mm long, about twice as long as wide. Paratype with pharynx extending to setiger 3, proventricle with about 35 narrow muscle cell rows, occupying setigers 3 through 5, 0.17 mm long, about twice as long as wide.

Etymology.—The specific name refers to the pair of mangrove islands, Twin Cays, where the type locality, West Bay, is located.

Remarks.—The description is of the holotype unless otherwise indicated. *Odontosyllis twincayensis* is distinguished from all previously described species of the genus by the unique combination of an occipital flap, a trepan with six teeth, a large bulbous proventricle with about 35 to 44 muscle cell rows, and serrated, bidentate setal blades of only one type. Furthermore, the setal blades are longer than those of most *Odontosyllis* species, and are unique in having the shape of a low triangle, a straight to slightly convex cutting edge with coarse serrations, and a bidentate tip with small, nearly equal terminal and subterminal teeth.

Odontosyllis twincayensis resembles *O. longigulata* Perkins, 1981, by having a trepan with six teeth and similar bidentate setal blades, but differs by having a well-developed, clearly defined occipital flap rather than a slight anterior peristomial fold, a proventricle with about 44 muscle cell rows rather than 60–70, and aciculae with pointed rather than blunt truncate tips. The new species is similar to *O. longiseta* Day, 1973, in having an occipital flap, a trepan with six teeth, and long serrated, bidentate setal blades, but differs by having a proventricle with about 44 muscle cell rows, rather than 60, and setal blades that are somewhat triangular with a length-to-width ratio of about 4.0, rather than elongate with nearly parallel edges and a length-to-width ratio of 7.8.

Odontosyllis twincayensis also resembles *O. glandulosa* Augener, 1913, and *O. gravelyi* Fauvel, 1928, particularly with regard to the length and bidentate aspect of the longest setal blades in these species, but differs by having a much more triangular setal blade bearing coarse serrations, rather than a slender elongate blade with nearly parallel edges and a smooth cutting edge or one bearing very fine serrations. *Odontosyllis twincayensis* is further distinguished from these two species by having a distinct well-developed occipital flap and only one type of bidentate setal blade.

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ORBINIIDAE (ANNELIDA: POLYCHAETA) FROM MANGROVE ROOT-MATS IN BELIZE, WITH A REVISION OF PROTOARICIIN GENERA

Vivianne Solis-Weiss and Kristian Fauchald

Abstract.—Benthic samples taken in root-mats of *Rhizophora mangle* contain four species of orbiniid polychaetes including *Naineris setosa,* and three new taxa, *Protoaricia pigmentata,* new species, *Pettibonella multiuncinata,* new genus and new species and *Pararicia belizensis,* new genus and new species. Recognition of the new genera lead to a preliminary phylogenetic analysis of the genera of the subfamily Protoariciinae, brief characterizations of all genera in the subfamily and the development of a key to genera of the Protoariciinae from world-wide areas.

The mangrove fauna of Twin Cays, Belize, has been under study for several years by a team of scientists under the direction of Dr. Klaus Rützler of the Smithsonian Institution. As part of this overall program, a study of the fauna of the root-mats of red mangroves, especially where these are covered by the green alga, *Caulerpa verticillata* was undertaken by Brian F. Kensley and Kristian Fauchald. The ecological findings will be reported elsewhere (Kensley & Fauchald, in preparation). This paper is the first report on the polychaetes collected during the study; several additional papers are in preparation.

Members of the family Orbiniidae have been reported from sandy and muddy environments world-wide. The subfamily Orbiniinae has been revised repeatedly (Day 1977, and references therein). The subfamily Protoariciinae has been less comprehensively treated. The presence of three new protoariciin taxa in material collected in Belize, including two that did not belong to any known genus, caused us to review the generic subdivision of the subfamily, to update and clarify as much as possible definitions and to attempt a phylogenetic analysis of the subfamily. The subfamily is here considered monophyletic; a dubious assumption, but without access to very much larger materials than was currently available a more detailed study is not possible.

Materials and methods.—The material was collected by K. Fauchald and B. F. Kensley as part of SWAMP (Smithsonian Western Atlantic Mangrove Program), directed by Dr. Klaus Rützler. The sample localities include West Bay, Twin Cays, and the mainland side of the middle islands in Blue Ground Range (Fig. 1). The habitat sampled was covered with red mangrove forest (*Rhizophora mangle*) varying in height from approximately 1.5 to 5 m and in density from open, isolated trees to dense forest with complete canopies. The microhabitat sampled was the root-mat where this mat was covered with a mat of *Caulerpa verticillata.* Part of the study includes a series of quantitative samples taken over a two-year period from 1979–1981. The samples were taken with a 10.4 cm diameter corer to a depth of approximately 10 cm in the substrate. The resulting core of the peat-like root-mat was gently broken up and screened through a 0.5 mm screen and preserved immediately in 10% neutralized formalin to which had been added Rose Bengal. After

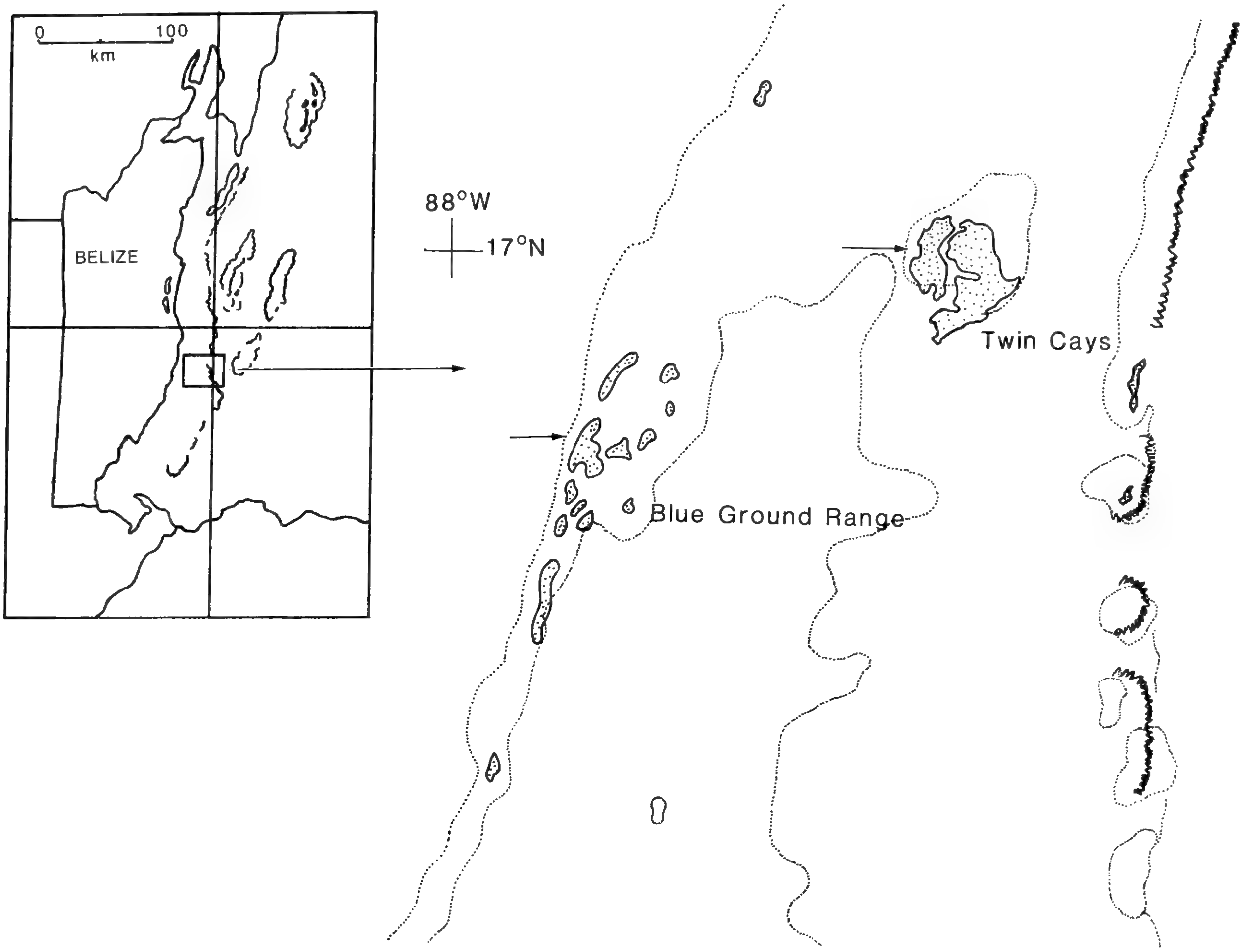


Fig. 1. Study area in Belize. The box to the left indicates the position of the study areas in relation to Belize; the study area is enlarged on the right. The two arrows in the enlargement indicates West Bay, Twin Cays and the un-named cay in the Blue Ground Range at which the collections were made.

24 hours in fixative, the samples were rescreened, and the specimens were sorted out in sea water, washed in freshwater and transferred to 70% alcohol. The samples were later sorted to family and counted.

All illustrations were made with the aid of a camera lucida attached to a stereo or compound microscope.

The morphological terminology is derived from Hartman (1957), Pettibone (1957) and Fauchald (1977). Any new terms used are explained in context. The literature cited include only papers directly used in this study; other papers can be found in the literature sections of the three papers mentioned above. The cladistic analysis was run using the IBM microcomputer version of PAUP 2.4; details are indicated below in the section on cladistic analysis of the genera. The terminology follows the one established by Wiley (1981). The character-list is given in Appendix 1 and the original data table in Table 2.

Station list.—As indicated above, all stations were taken in two locations; each sample consisted of a single numbered core; the core numbers for each of the two localities are given below.

West Bay, Twin Cays, Belize, 10–50 cm water depth; root-mat of *Rhizophora mangle,* covered with *Caulerpa verticillata* core numbers M-1, M-2, M-3, M-5, M-9, M-10, M-11, M-12, M-27, M-32, M-35, M-50, M-51, M-55, M-58, M-59, M-70, M-71, M-88, M-90, M-95, M-96, M-102, M-105, M-107, M-133, M-136, M-137, M-139, M-140, M-142, M-143, M-144, M-145, M-146, M-147 and M-148.

West side of middle cay, Blue Ground Range, Belize, 10–50 cm water depth; root-

Table 1.—Variability of selected morphological features of *Pettibonella multiuncinata*. All specimens included.

	Range	Mean	SD
Length in mm	1–20	8.01	5.21
Number of setigers	31–110	66.83	27.12
Number of thoracic setigers	7–18	12.34	3.36
Branchiae from setiger number	6–16	9.9	4.18
Maximum number of rows of thoracic neuropodial uncini	2–5	3.3	0.79
Maximum number of uncini per row, thoracic neuropodia	2–7	4.16	1.39
Abdominal thin hooks first present from setiger number	7–19	13.20	4.63
Abdominal large hooks first present from setiger number	6–22	14.57	3.69

mat of *Rhizophora mangle,* covered with *Caulerpa verticillata,* core numbers M-23, M-24, M-78 and M-79.

In addition to the material newly identified from the collections in Belize, we also examined type material and other materials as needed to verify our identifications and to clarify taxonomic uncertainties. This material is listed as previously identified material for each species.

Systematic Results

Family Orbiniidae Hartman, 1942

The two subfamilies, Orbiniinae and Protoariciinae are currently separated only by the presence of one or two asetigerous anterior segments (Fauchald 1977).

Subfamily Orbiniinae Hartman, 1957

Key to genera of this subfamily can be found in Day (1977).

Genus *Naineris* Blainville, 1828

Naineris setosa (Verrill, 1900)

Figs. 2–3

Aricia setosa Verrill, 1900:651–653.

Anthostoma latacapitata Treadwell, 1901: 203–205, figs. 61–65.

Naineris setosa.—Hartman, 1942:61, figs. 116–118.—Hartman 1951:67–70, pl. 17, figs. 1–6.—Hartman, 1957:305, pl. 41, figs. 1–6.

Material examined.—Previously identified material: Bermuda, Platts Inlet, 1898, coll. A. E. Verrill and party (1 incomplete syntype, YPM 1242). Bermuda, 1901, coll. A. E. Verrill and party; id. M. Pettibone, 1962 (one incomplete specimen, YPM 1384). Bermuda, 1903, coll. W. R. Coe; id. M. Pettibone, 1962 (one complete specimen, YPM 1303). Bermuda; id. M. Pettibone (one incomplete specimen, USNM 34092). Bermuda, SE of Causeway, 1979, coll. & id. S. Gardiner (12 specimens).

Newly identified material: Belize, West Bay, Twin Cays and Blue Ground Range, 1979–1981, coll. K. Fauchald and B. F. Kensley M-11 (5, USNM 120928); M-12 (1, USNM 120932); M-23 (2, USNM 120935); M-24 (1, USNM 120938); M-90 (1, USNM 120955).

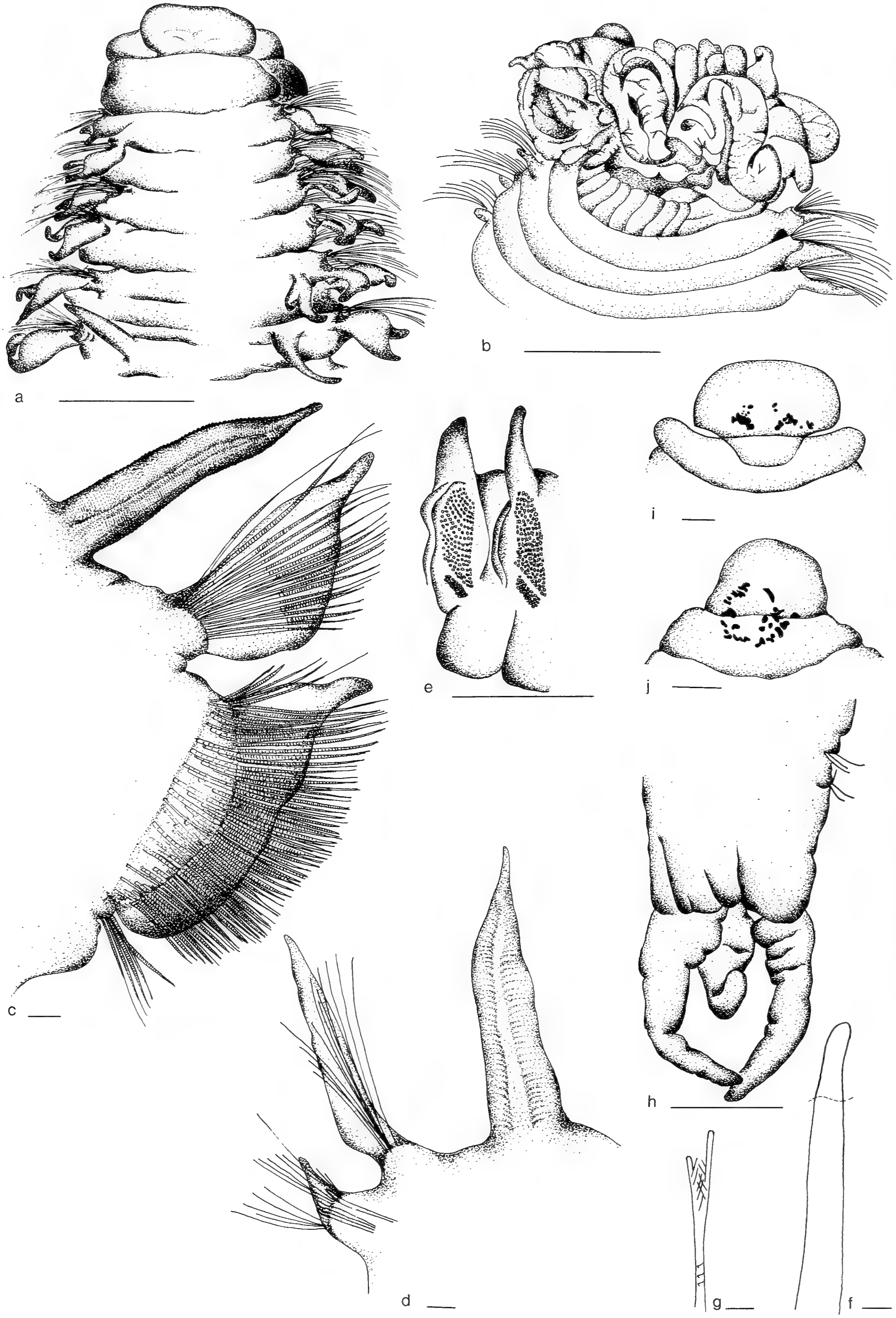
Description.—The description is based on the specimen referred as the syntype above, supplemented by notes on other material. No additional type material is currently available. The syntype is an incomplete fragment of 150 segments measuring 58 mm. It is widest at midthorax, 1.63 mm without, 3.83 mm with parapodia; the anterior abdomen is 1.53 mm without and 2.83 mm with parapodia; the posterior abdomen is 1.33 mm without and 2.4 mm with parapodia. Color as preserved, brown.

The prostomium is broadly truncate to T shaped (Fig. 2a). Two diffuse, deeply embedded eyespots are present. Two shallow, comma-shaped grooves are present dorsally at the posterior end of the prostomium.

The peristomium is a broad, asetigerous

Table 2.—Character-states scored for protoariciin genera. Inappropriate or missing information marked with a dash.

Orbiniella	2	0	0	0	0	2	2	2	2	2	2	0	0	1	–	2	0	1	2	1	1	1	1	2	2	1	1	–	–	1	2
Proscoloplos	2	8	2	1	1	2	2	2	2	2	2	1	2	2	–	1	1	2	2	1	2	2	2	1	2	1	2	4	1	1	2
Protoaricia	2	–	3	1	2	1	1	2	1	1	1	1	1	2	0	1	1	1	1	1	1	2	2	2	2	1	1	4	1	2	1
Protoariciella	2	6	4	2	2	2	2	1	2	2	1	1	–	2	–	2	1	2	1	1	–	2	1	2	1	–	1	6	1	2	2
Schroederella	1	–	–	1	2	2	2	2	2	1	1	3	1	1	7	1	2	2	1	1	2	2	1	2	2	1	1	4	1	2	1
Pettibonella	3	9	1	2	2	2	2	2	2	1	1	1	2	2	3	1	2	2	2	2	2	2	2	1	1	2	2	4	2	2	2
Pararicia	2	6	3	1	2	1	2	2	2	2	1	1	1	2	0	1	1	1	2	1	2	2	1	2	2	1	2	4	1	3	2
Scoloplella	1	–	4	–	2	2	2	2	2	2	2	2	1	1	–	–	2	2	2	1	2	2	2	2	2	2	–	–	–	1	–
Leitoscoloplos	1	8	1	2	2	2	2	2	2	2	2	1	2	2	0	2	1	1	2	1	2	2	2	2	2	0	2	2	1	2	2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segment; the mouth is more than ⅔ of the total width of the peristomium. The eversible pharynx is not everted in the syntype; it is eversed and illustrated as present in another Bermudian specimen (YPM 1303, Fig. 2b).

The thorax consists of 20 biramous setigers, fully developed by setiger 5. The notopodial postsetal lobes are foliaceous, broadest at two-thirds distance from the base. The neuropodial postsetal lobes are shorter, broader and rounder than corresponding notopodial lobes. They bear an upper digitiform papilla which is longer anteriorly than posteriorly (Fig. 2c). Statocysts are visible as oval spots dorsally, anteromedial to the branchiae. Setigers 21 to 25 are transitional, characterized by a diminishing number of neuropodial setae both in number of rows and in number of setae in each row. The parapodia become gradually more dorsal. The abdomen begins at setiger 25. The notopodial postsetal lobes become slenderer and progressively shorter towards the posterior abdomen. The corresponding neuropodial lobes become sharply reduced in size and foliaceous in shape (Fig. 2d), instead of round. Low dorsal ridges are present from the beginning of the abdomen, becoming less conspicuous towards the end of the fragment. No neuropodial subpodial lobe is present either in anterior or middle abdominal segments.

Branchiae appear, in all specimens studied, in setiger 6. However, in the syntype, a stout, unpaired bifid structure is found on one side in the position where branchiae are located on later setigers. This feature seems to be an abnormality of the specimen rather than a feature normally associated with the species (Fig. 2a). From setiger 6, normal paired branchiae appear. They are digitiform, elongate, held erect over the body or recumbent along the dorsum. They are similar in length to the notopodial lobes but slenderer in the thoracic region, whereas in the abdominal region they are longer and broader than the corresponding notopodial lobes. They are present to the end of the fragment, and to the end of the body in all the complete specimens.

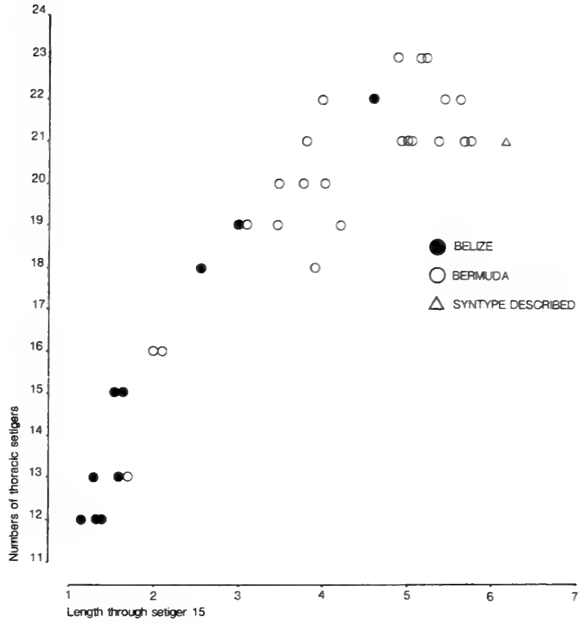

Fig. 3. Relationship between length through setiger 15 and number of thoracic setigers in *N. setosa* from Belize and Bermuda.

The thoracic notopodia have long crenulate capillary setae aligned in about three irregular rows and totalling approximately 25 or 30 setae per notopodium. The neuropodial thoracic setae are all crenulate capillaries. They are shorter than the notopodial setae and positioned in two bundles: 1). Approximately eight irregular, longitudinal palisaded rows, each bearing about 25 such setae, and 2). Approximately four irregular

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Fig. 2. *Naineris setosa*: a, Anterior end of syntype, dorsal view; b, Anterior end of syntype, YPM 1303, showing evaginated pharynx; c, Right parapodium setiger 12, syntype, anterolateral view; d, Left parapodium, setiger 49, syntype, anterolateral view; e, Right parapodia, setigers 17–18, syntype, dorsal view; f, Abdominal uncinus, setiger 49, syntype; g, Furcate seta, abdominal setiger, CBC-M-11; h, Posterior end, CBC-M-11; i, Anterior end, dorsal view, CBC-M-11; j, Anterior end, dorsal view, CBC-M-90. Scales: a, b, e, 1 mm; c, d, h–j, 100 μm; f, g 10 μm.

diagonal palisaded rows, posterior to the first bundle, each bearing 14 to 18 setae (Fig. 2e). In the abdomen, the number of setae decreases to about a dozen or less in both rami, although they are more abundant in the notopodium than in the neuropodium. Furcate setae are present in some abdominal notopodia but are difficult to observe. They have a delicately spinous shaft and two distal tines of different length (Fig. 2g). In the abdominal neuropodia, in addition to the crenulate setae two or three straight, bluntly pointed uncini appear (Figs. 2d, f).

The syntype is incomplete, and the only complete specimen from YPM, has a damaged pygidium. The pygidium in a complete specimen from Belize (CBC-M-11, Fig. 2h) is elongate with three (probably originally four) elongate distally tapering anal cirri. Anal aperture is terminal and central.

Comparison of specimens from Belize and Bermuda.—The specimens newly identified agree fairly well with both type material and earlier descriptions. The main differences noted are:

1) The prostomium can be either T shaped or rounded.

2) In specimens with rounded prostomia numerous eyes are present, scattered between the middle and the posterior end of the prostomium (Fig. 2i). In specimens with T shaped prostomia, the eyespots are formed into two to four sickle shaped dark areas located at the posterior end of the prostomium; occasionally some additional small isolated spots are present (Fig. 2j).

3) The number of thoracic setigers varies from 13 to 23.

4) The two separate groups of thoracic neurosetae are distinct only in larger specimens. Smaller specimens have only one bundle with fewer rows and fewer setae per row than in the syntype.

In order to determine if the number of thoracic setigers and the shape of the prostomium are size-related features, we did a least squares regression correlating the number of thoracic setigers of the specimens with the length of the 15 first setigers. The results show a high correlation between the two ($r = 0.91$). There is no significant correlation between the different prostomial shapes and the size of the organism ($r = 0.37$).

Figure 3 shows that in general, the Belize specimens reach maximum number of thoracic setigers at a smaller size than do the Bermuda specimens. There is no consistent trend in relation between numbers of thoracic setigers and length in the material from Bermuda. Especially the syntype is very long in relation to the number of thoracic setigers. The differences among the populations are not sufficient to recognize them, even at the subspecies level, but are useful in allowing us to expand and quantify the description of the species.

Hartman (1957) stated that neuropodial subpodial lobes should be present in this species; a feature not mentioned by Verrill (1900) in the original description nor mentioned in any other review. We examined part of the material listed by Hartman (1957) including the specimens used to make the illustrations for that paper and failed to find subpodial lobes in any of the specimens. We assume that the subpodial lobes as mentioned and illustrated by Hartman (1957) represent a *lapsus calami,* and that such lobes are normally absent in the species.

Habitat.—Subtidal, probably euryhaline species associated with vegetation (*Thalassia testudinum* beds, algal mats and *Rhizophora mangle* root-mats). Substrate may be sandy, sandy mud, or mangrove root-mats with minimal sediment. Locally present both in West Bay, Twin Cays and at Blue Ground Range (Fig. 1).

Distribution.—*N. setosa* has been reported from Bermuda (type locality), various localities in the Gulf of Mexico (Perkins & Savage 1975; Hernandez-Alcántara & Solis-Weiss 1989), Puerto Rico (Treadwell 1901), and Acapulco, Mexico (Hartman 1957).

Subfamily Protoariciinae Hartman, 1957

Preliminary Phylogenetic Analysis of the Protoariciin Genera

This analysis of putative relations among the protoariciin genera is based on several assumptions. First, the subfamily is assumed to be monophyletic; this assumption cannot be justified without a complete analysis of the whole family, or indeed the order to which the family will eventually be referred (its current assignment is unsatisfactory).

A second major set of assumptions can be summarized by the choice of the genus *Leitoscoloplos* among the Orbiniinae as outgroup. Members of this genus are characterized first and foremost by lacking all modified setae in the thorax, and by the extreme simplicity of the acicular spines in the abdomen, in addition to the simple structure of the parapodial lobes and branchiae. The choice thus polarizes all more complex features, such as the presence of complex parapodial lobes, the presence and structure of various kinds of thoracic hooks and even the loss of certain features, such as branchiae, as apomorphic features. The procedure has the advantage of simplicity: without information to the contrary, it appeared simpler to assume that all more complex features were apomorphic, rather than randomly select some as being plesiomorphic and others as apomorphic. Resolution of this issue cannot come until possible relations among all orbiniids and between the orbiniids and the related families have been analyzed in detail.

The features used to characterize the genera are those traditionally used in orbiniid systematics (Day 1954, Fauchald 1977). The initial list contained 41 characters; the list was reduced to 31 characters by exclusion of features invariant among the taxa considered (including the outgroup) and of certain features that were so poorly known for most members of the group that they could not be coded (numbers of abdominal segments present for example). Appendix 1 lists the characters and character-states included in the analysis. Multistate characters are listed as transformation-series.

The character matrix was run on PAUP using the ALLTREES option (cfr. documentation for PAUP as issued with the program).

Four trees were found, the consistency index was 0.670 and length was 88 for all four. All four trees plus a consensus tree is presented in Fig. 4. The four trees have several features in common. *Protoariciella, Schroederella* and *Scoloplella* are grouped together in all four trees. *Orbiniella* which is mainly characterized by the loss of various features, nevertheless is defined by unique autapomorphies. In three of the four trees, *Protoaricia* and *Pararicia* show a unique synapomorphy and emerge jointly; in the last tree this character-state is interpreted as having being a reversal. In all four trees the two genera emerge next to each other. The presence of the curved hooks (called swan-shaped in *Proscoloplos*) is a unique synapomorpy joining *Pettibonella* and *Proscoloplos.*

All internal nodes are supported by various apomorphies in all four trees. All four trees are defined by synapomorphies. None of the nodes is exclusively supported by reversals or parallellisms, or exclusively by synapomorphies created by various states in transformation series. All tree-topologies and a strict consensus tree are shown in Fig. 4. All taxa, including the two genera are supported by autapomorphies.

The consensus tree demonstrates that the summary given above cannot be expanded upon. The character-sequence used to define the four trees differ and different transformation-series have been reversed in each tree. Without additional information the "correct" reading of this series cannot be confirmed.

The analysis was undertaken to examine

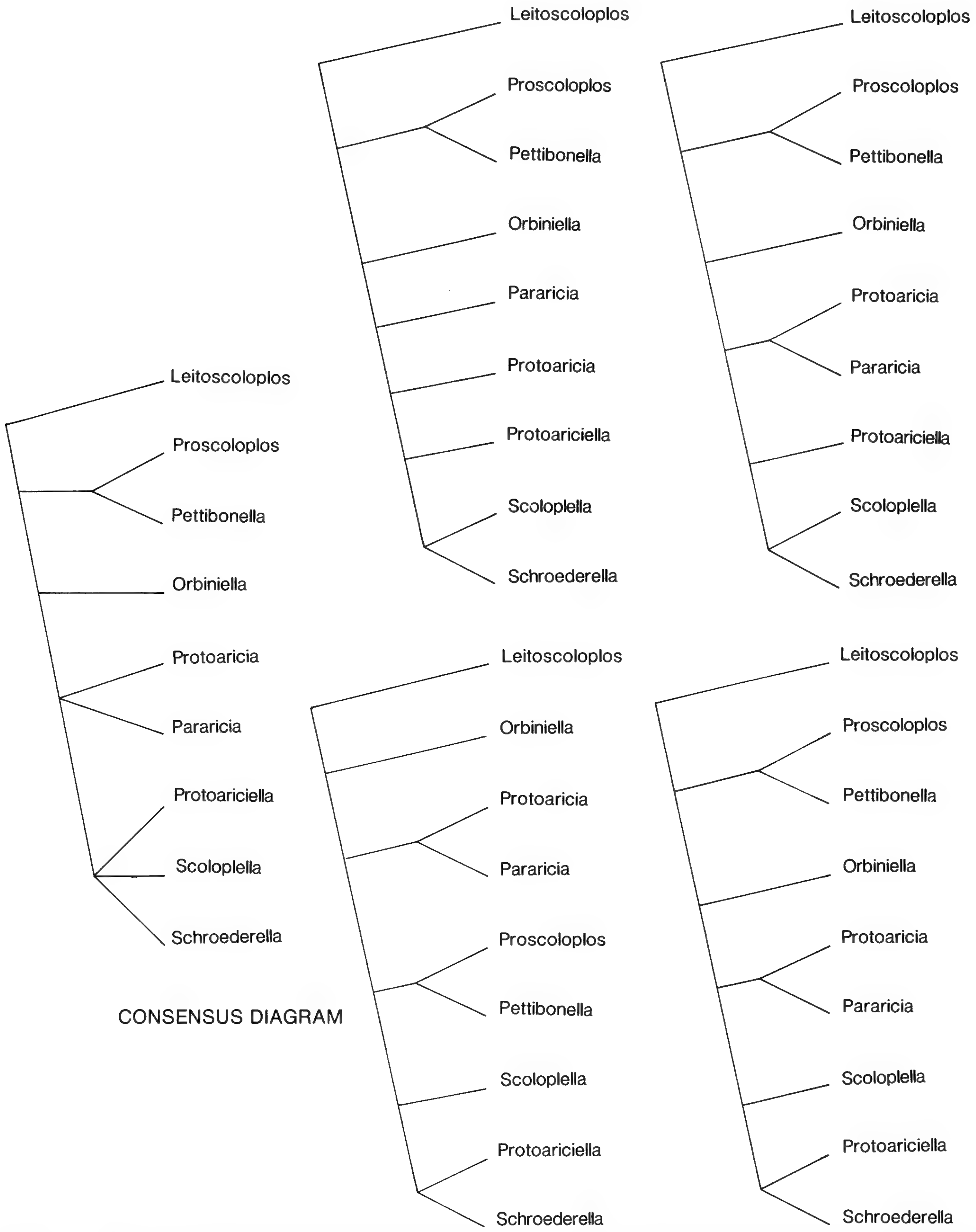

Fig. 4. Cladograms showing possibly phylogenetic relations among the genera of the Protoariciinae. Further explanation in the text.

the level of support for previously described genera and compare them to the newly described genera. We feel justified in erecting the new genera: They represent unique combinations of features otherwise not present in the subfamily, but recognize that the validity of all genera may again be tested when the whole family is being analyzed.

Key to Genera of Protoariciinae

1. Branchiae absent .... *Orbiniella*
– Branchiae present 2
2. Transition between thorax and abdomen indistinct ...... *Protoariciella*
– Transition between thorax and abdomen distinct, transitional segments may be present 3
3. Only crenulated capillaries present .... *Scoloplella*
– Crenulated capillaries and other kinds of setae present 4
4. Abdominal hooks acicular 5
– Abdominal hooks otherwise 7
5. Prostomium acutely pointed; anus dorsal .... *Schroederella*
– Prostomium distally rounded; or bluntly conical; anus terminal 6
6. Thorax with mucronate setae and subuluncini in addition to crenulated capillaries .... *Protoaricia*
– Thorax with crenulated capillaries only .... *Pararicia*
7. Abdominal hooks of a single kind .... *Proscoloplos*
– Abdominal hooks of two different kinds .... *Pettibonella*

Brief Generic Characterizations

The new genera are defined in place in the text.

Orbiniella Day, 1954, type species *O. minuta* Day, 1954. Prostomium rounded or pointed. Branchiae absent. All thoracic setae crenulate. Thoracic notopodial setal lobes indistinct; notopodial postsetal lobes reduced; neuropodial postsetal lobes single, rounded. Two transitional segments present. Abdominal setae crenulated capillaries, acicular setae and sometimes furcate setae. Anus terminal.

Proscoloplos Day, 1954, type species *P. cygnochaetus* Day, 1954. Prostomium rounded. Eyes absent. Branchiae from setiger 8. All thoracic setae crenulated capillaries. Thoracic notopodial setal lobes indistinct. Notopodial and neuropodial postsetal lobes tapering. Abdominal setae crenulated capillaries and one or two swan-shaped hooks. Anus terminal with four tapering anal cirri.

Protoaricia Czerniawsky, 1881, type species *Aricia oerstedi* Claparède, 1864. Prostomium rounded. Two eyes. Branchiae limited to abdominal segments. Thoracic setae crenulated capillaries, hooks and subuluncini. Thoracic notopodial setal lobes distinct. Notopodial and neuropodial postsetal lobes tapering. No transitional segments present. Abdominal setae crenulated capillaries and neuropodial uncini. Anus terminal with four blunt anal papillae or anal cirri absent.

In the original description of the type species, Claparède (1864), stated that the dorsal (notopodial) rami in the abdomen were bifurcate; no types are available of any of Claparède's species (cfr. Fauchald, in prep.). Specimens from the Mediterranean Sea (off Málaga, Spain and off Marseille, France lack bifurcate abdominal notopodia (see discussion below).

Protoariciella Hartmann-Schröder 1962a, type species *P. uncinata* Hartmann-Schröder, 1962a. Prostomium rounded. Two eyes. Branchiae from setiger 6 or 8. Thoracic notosetae all crenulated capillaries. Abdominal notosetae crenulated capillaries and acicular setae. Neurosetae include crenulated capillaries, thick, tridentate hooks, slender acicular setae with flattened teeth and thick, smooth spines. Separation between thorax and abdomen indistinct. Anus terminal; anal cirri absent.

Schroederella Laubier, 1962, type species *S. pauliani* Laubier, 1962. Prostomium

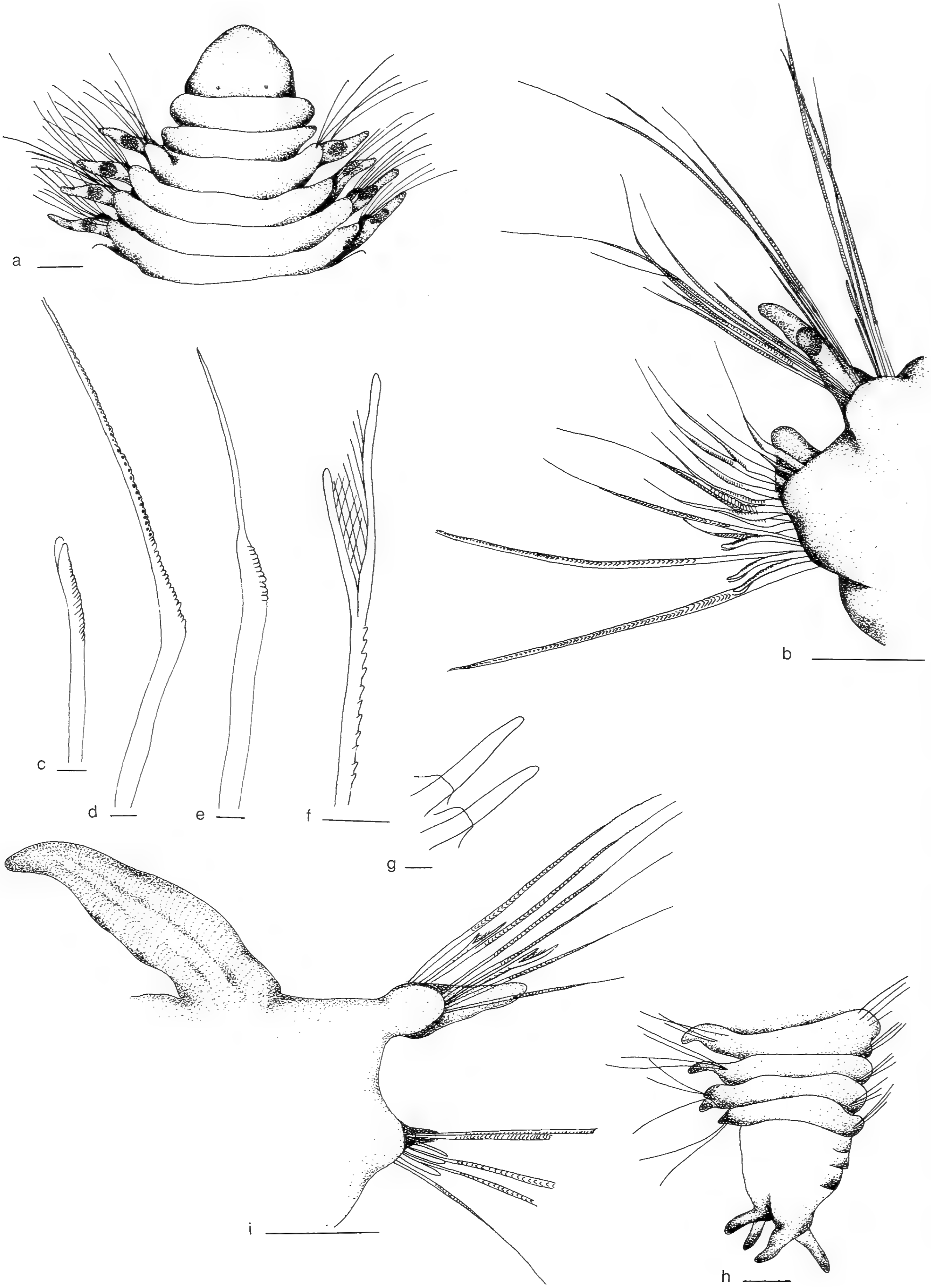

Fig. 5. *Protoaricia pigmentata*: a, Anterior end, holotype, dorsal view; b, Left parapodium, setiger 6, holotype, anterolateral view; c, Hooded hook, setiger 5, holotype; d, Subuluncinus, setiger 5, holotype; e, Mucronate seta,

acutely pointed. Two eyes. Branchiae on abdomen only. Parapodia poorly developed; thoracic notopodial postsetal lobes digitiform, increasing in size posteriorly; thoracic neuropodial postsetal lobes single, rounded. Thoracic setae crenulated capillaries and straight neuropodial uncini. Abdominal notopodial and neuropodial postsetal lobes tapering. Abdominal setae crenulated capillaries and slender, pointed notopodial aciculae and hooded, thick neuropodial aciculae. Transitional segments present. Anus distinctly dorsal with 4 anal lobes.

Scoloplella Day, 1963, type species *S. capensis* Day, 1963. Prostomium pointed. Eyes absent. Branchiae present from mid-abdominal segments. All postsetal lobes rounded. Parapodial rami reduced. All setae crenulated capillaries. Anus terminal.

The genus *Scoloplosia* proposed by Rullier, 1972, was synonymized with *Protoaricia* by Ben-Eliahu (1976). This synonymy is here accepted.

Genus *Protoaricia* Czerniawsky, 1881

Protoaricia pigmentata, new species

Fig. 5

Material examined.—M-78 (one, holotype, USNM 120950, two paratypes, USNM 120951); M-79 (three paratypes, USNM 120952, one paratype Australian Museum; three paratypes British Museum (NH) and two paratypes Zoological Museum Hamburg).

Description.—Holotype with 8 thoracic and 55 abdominal setigers for a total of 63; transitional setigers absent. Total length 5.4 mm; width at midthorax 0.8 mm and 0.54 mm in posterior abdomen. Length of other types 3 to 6.5 mm. Body somewhat flattened dorsoventrally; widest at midthorax. Color, as preserved, white with scattered brown dorsal pigmentation in branchial region to mid-abdomen in some specimens. Brown, circular postsetal patch on each notopodial thoracic lobe about two thirds from base, through mid-abdomen in most specimens (Fig. 5a, b).

Prostomium frontally round and wider at base. Two small round eyes deeply embedded, occasionally very difficult to see; located towards peristomial boundary (Fig. 5a). Peristomium and asetigerous segment clearly defined on all sides. Mouth, with lateral lips more than two thirds of ventral peristomial width. Pharynx not everted in any specimen.

All parapodia biramous. Thoracic notopodial postsetal lobes elongate, cirriform; widest at proximal two-thirds of length (Fig. 5b). Thoracic neuropodial postsetal lobes shorter, wider and rounder than corresponding notopodial lobes; upper digitiform papillae present on lobes (Fig. 5b). Abdominal parapodia located slightly more dorsally than thoracic ones (Fig. 5i). Abdominal notopodial postsetal lobes similar to thoracic notopodial postsetal lobes; becoming reduced in far posterior setigers. Abdominal notopodial and neuropodial postsetal lobes reduced last one to four setigers; upper papillae of neuropodia elongate; cirriform in anterior and mid-abdomen; shorter in far posterior setigers.

Branchiae in holotype from setiger 8; missing on last two setigers; in paratypes from setigers 6–9 and missing in last two to four setigers; foliaceous, spionid-like, elongate, never overlapping; recumbent (Fig. 5i). First pair shorter and slenderer than other branchiae. Branchiae longer and wider than notopodial lobes through mid-abdomen; thereafter distinctly reduced and more cirriform.

Thoracic notopodial setae distinctly long-

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setiger 5, holotype; f, Abdominal furcate notoseta, holotype; g, Abdominal neuropodial uncinus, holotype; h, Posterior end, dorsal view, holotype; i, Right parapodium, setiger 36, from one of the paratypes, anterolateral view. Scales: a, b, h, i, 100 μm; c–g, 10 μm.

er than abdominal notopodial setae; capillary crenulate setae long, slender and more abundant in thorax than in abdomen; furcate setae present from thorax (Fig. 5f); single or at most two in a notopodium. Thoracic neuropodial capillary crenulate setae shorter than corresponding notosetae; three or four mucronate setae, up to five subuluncini and up to three thinly hooded, distally tapering hooks present in thoracic neuropodia (Figs. 5c–e). Mucronate setae in upper end of setal bundles; subuluncini in middle and hooks in lower end of bundles (Fig. 5b). In the abdomen only three to five crenulate and one or two furcate neurosetae present; subuluncini, mucronate setae and hooded hooks absent; two to three slightly sigmoid, distally tapering hooks without hoods present (Figs. 5i, g).

Pygidium elongate with four large papillae; each terminated by a slender digitiform cirrus of variable length (Fig. 5h). The anal aperture is central and terminal. Tubes absent.

Etymology.—The specific name refers to the characteristic brown color patterns present in specimens of this species.

Discussion.—Among the described species of *Protoaricia,* this species resembles *P. oerstedi* (Claparède) and *P. capsulifera* (Bobretzky) more than *P. minima* (Rullier). The types of *P. oerstedi* and *P. capsulifera* are unavailable. The discussion is based on the original descriptions and illustrations and in the case of *P. oerstedi,* on observations on specimens from the Mediterranean Sea (Cap Couronne, near Marseille, France and near Málaga, Spain).

According to the literature (Claparède 1864, Bobretzky 1870, Eisig 1914, and Fauvel 1927), *P. oerstedi* and *P. capsulifera* are much larger (13 to 15 mm) than *P. pigmentata. P. capsulifera* and *P. pigmentata* have very short segments, up to 77 for 6 mm in length; in contast *P. oerstedi* has only 52 segments for the same length.

In descriptions of *P. oerstedi,* branchiae are said to begin on the first abdominal setiger, reported as setiger 12, the abdomen is flattened posteriorly, notopodial lobes are bifurcate and two or three straight aciculae are present in the posterior notopodia; only one to two uncini are reported present in each abdominal neuropodium (Claparède 1864, Eisig 1914, Fauvel 1927). In the Mediterranean material however, branchiae begin well after the first abdominal setiger (12–14, but the thorax has only six to nine setigers).

In *P. pigmentata* the abdomen is nearly cylindrical; the notopodial lobes are never bifurcate; distinct abdominal aciculae are absent and we commonly found three abdominal neuropodial uncini, even in small specimens. Branchiae are present from the last thoracic setiger.

Possible differences in pygidial structures present a problem: Bobretsky's illustration of *P. capsulifera,* shows the pygidium to be very similar to that of *P. pigmentata.* Fauvel's illustration of the pygidium of *P. oerstedi* is in lateral view, making it impossible to determine accurately the distribution and length of various papillae; Fauvel's description is uninformative in that it only refers to the pygidium as having four short round cirri. The Mediterranean specimens have all short anal papillae rather than distinct cirri. Statocysts are present in both *P. oerstedi* and *P. capsulifera* and absent in *P. pigmentata.* In the description of *P. capsulifera,* no mention is made of the mucronate setae or subuluncini, nor are they illustrated.

Rullier (1972) did not mention the number of thoracic setigers, the shape of the thoracic region, or the shape of the pygidium for *P. minima.* Rullier (1972) reported branchiae absent and on the strength of this feature created a new genus, *Scoloplosia* for it: Ben-Eliahu (1976) synonymized it with *Protoaricia* since her largest specimen of the same species had branchiae "from setigers 13 to 16"; that is, from one of the abdominal setigers as in the other species of *Protoaricia.* In addition, *P. minima* differs from our specimens in the following characters: Eyes are absent in *P. minima.* The branchiae, are fingerlike from the start in *P. minima,* not foliaceous as in *P. pigmentata.* Ben-Eliahu (1976) did not mention presence of mucronate setae for *P. minima* and Rullier (1972) specifically stated that subuluncini and mucronate setae were absent in his material. *P. minima* also has one or two abdominal neuropodial uncini rather than three as present in *P. pigmentata.*

Distribution.—The species is known only from Blue Ground Range, Belize (Fig. 1).

Pettibonella, new genus

Diagnosis.—Prostomium rounded or conical, usually with two eyespots. Two anterior asetigerous segments. Branchiae deciduous, present from thoracic region, becoming longer than notopodial postsetal lobes in abdominal region. Notopodial postsetal lobes well developed in thorax and abdomen, neuropodial postsetal lobes well developed only in thorax. Notosetae include crenulate capillaries only. Neurosetae in thorax and abdomen include crenulate capillaries (shorter than notosetae) and uncini in thorax; a few crenulate capillaries and two different kinds of dentate hooks in abdomen. The pygidium with four digitiform anal cirri.

Because of obvious close similarities between *Proscoloplos* and *Pettibonella,* we compared *Proscoloplos cygnochaetus,* the type species, and *P. confusus* Hartmann-Schröder, 1962b, the only other species in the genus, to our new species. The type material of *P. cygnochaetus* (British Museum (Natural History), ZK 1955.3.20.1–6) was examined as were the types of *P. confusus.*

In *Proscoloplos* eyes are absent, rather than present. Branchiae are rounded, with glandular cells and much shorter than in *Pettibonella.* Only a few crenulate capillaries are present in the thoracic setigers in *Proscoloplos*; these setae are abundant in *Pettibonella,* and in the latter there are, in addition, several neuropodial thoracic uncini. The distinctive swan-shaped hooks are present singly or at most paired in *Proscoloplos* and they differ little in size or shape where paired; in *Pettibonella* two kinds of hooks, differing in size and shape are present.

Etymology.—This genus is named in honor of Dr. Marian H. Pettibone, Emeritus Zoologist of the Smithsonian Institution, in recognition of her excellent work on polychaete systematics.

Type species.—*Pettibonella multiuncinata,* new species.

Pettibonella multiuncinata, new species

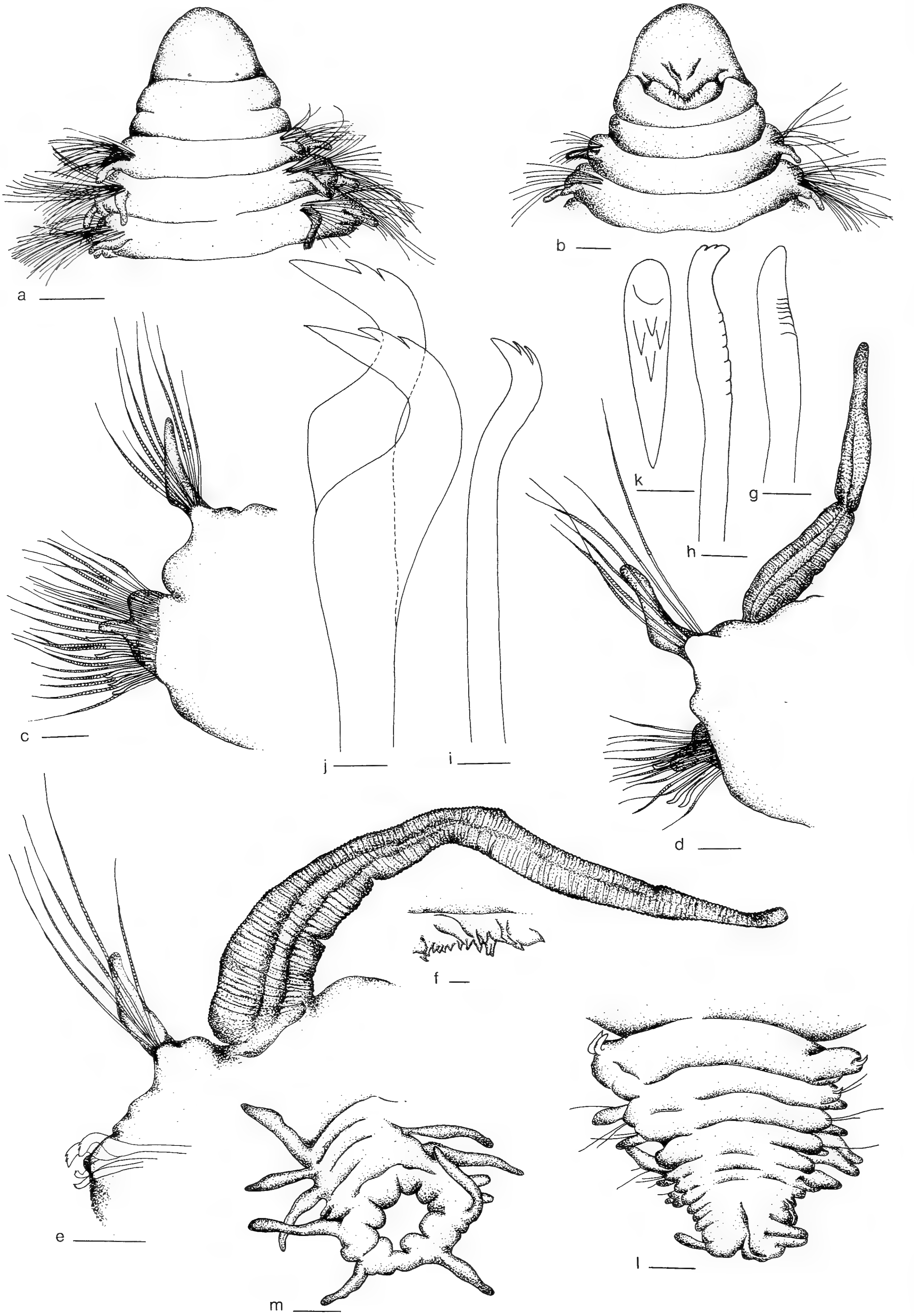
Fig. 6, Table 1

Material examined.—M-1 (one specimen); M-2 (1); M-3 (1); M-9 (one paratype, USNM 120926); M-11 (1); M-12 (8); M-23 (13); M-24 (1); M-27 (5); M-32 (1); M-35 (4); M-50 (2); M-51 (2); M-55 (8); M-59 (1); M-70 (1); M-71 (1); M-88 (4); M-90 (2); M-95 (3); M-96 (6); M-102 (1); M-105 (1); M-107 (1); M-139 (4); M-140 (3); M-142 (1); M-143 (3); M-144 (4); M-145 (1, holotype, USNM 120971, one paratype USNM 120972); M-146 (three paratypes, USNM 120973); M-147 (4); M-148 (1).

Description.—Holotype with 15 thoracic and 75 abdominal setigers, for a total of 90; total length 16mm, greatest width (in thorax) approximately 0.8 mm excluding parapodia. Body somewhat flattened dorsoventrally, especially in anterior region. Color as preserved, white.

Prostomium conical, with two deeply embedded eyespots near peristomial boundary (Fig. 6a). Peristomium partially fused ventrally to next segment. Mouth two-thirds of ventral width of peristomium; lips lateral (Fig. 6b). Pharynx not seen in any specimen. Division between asetigerous segments distinct laterally, indistinct dorsally or ventrally, but never simultaneously on both sides.

Branchiae from setiger 9; missing in last two setigers; elongate, flattened, broad based.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Some branchiae with middle constrictions (Fig. 6d). Branchiae deciduous with no obvious glandular cells; branchial surface with minute digitiform papillae (Fig. 6f). First branchiae shorter than notopodial lobes; increasing in length towards posterior end, becoming between three and five times longer than notopodial lobes (Fig. 6e). Most branchiae held erect over the dorsum; some recumbent. All parapodia biramous.

First notopodium with filiform postsetal papillae; first neuropodium with similar, somewhat shorter postsetal lobes. Following notopodial postsetal lobes increasing in length. From setiger 2 neuropodial postsetal lobes unequally bilobed; superior part distally rounded; inferior part digitiform and longer than superior part (Fig. 6c). Bilobed neuropodial postsetal lobes best developed at about setiger 5–6, decreasing towards end of thorax. Inferior part disappearing gradually towards end of thorax (Fig. 6d); absent in abdomen.

Thoracic setae of two kinds: crenulate capillary noto- and neurosetae, and neuropodial uncini. First setiger with a bundle of approximately 10 notopodial crenulate capillary setae, and 15 or more neuropodial crenulate setae in a fan-shaped array. Notopodial crenulate setae increasing in length, but numbers remaining roughly constant through thorax. Crenulate neurosetae increasing dramatically in numbers; becoming arranged in irregular rows forming fan-shape total arrays. Four rows of crenulated neurosetae present in setigers 5–6. In setigers 13–15 number of crenulate neurosetae decreasing to six or seven. In abdomen two short crenulate neurosetae present. From setiger 2 to end of thorax, up to five uncini in a vertical row ventralmost in each neuropodium. Uncini yellow, shafts straight; distally bent, blunt tipped; with 7–12 flattened transverse scales (Fig. 6g); tips sometimes worn resulting in tooth-like structures being formed (Fig. 6h). In transitional segments (13–15) uncini with two terminal teeth.

Transition from thorax to abdomen marked at setiger 16 by reduction in number of neuropodial crenulate setae and replacement of thoracic uncini by two tridentate hooks (Fig. 6i). Transition region also with reduction of postsetal lobes and progressively more dorsal position of parapodia.

Tridentate hooks without hoods located ventrally with cutting edges facing dorsally (Fig. 6i). Hooks of setiger 16 intermediate in shape between thoracic uncini and fully formed hooks of middle abdomen (i.e. teeth present but hooks more elongate than in following setigers). From setiger 17, another kind of hook present, facing the other two hooks in a vis-a-vis position. In setigers 17–20, all hooks increasing gradually in width, especially subterminally. Where fully developed, large hooks with large main fangs surmounted by four denticles in a rhomboid arrangement (Fig. 6j, k); shafts distinctly inflated below rostrum. Usually one large hook and two slender hooks in a setiger; occasionally and scattered, some setigers with two large hooks parallel to each other; facing either two or three slender hooks. Branchiae distinctly reduced and hooks are absent in last three parapodia and last two parapodia asetigerous.

Pygidium elongated with four slender, digitiform cirri; two dorsal cirri longer than ventral ones. Pygidial cirri retracted or

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Fig. 6 *Pettibonella multiuncinata*: a, Anterior end, holotype, dorsal view; b, Anterior end, holotype, ventral view; c, Left parapodium, setiger 6, holotype, anterolateral view; d, Left parapodium, setiger 12, holotype, anterolateral view; e, Left parapodium, setiger 60, holotype, anterolateral view; f, Branchial edge, setiger 60, holotype; g, Thoracic uncinus, setiger 6, holotype; h, Thoracic uncinus, setiger 12, holotype; i, Slender neuropodial abdominal hook, setiger 82, holotype; j, Large neuropodial abdominal hook, setiger 82, holotype; k, Large neuropodial abdominal hook, setiger 82, holotype, view from distal end; 1, Posterior end, ventral view, holotype; m, Pygidium, CBC-M-9. Scales: a–e, l, m, 100 μm; f–k, 10 μm.

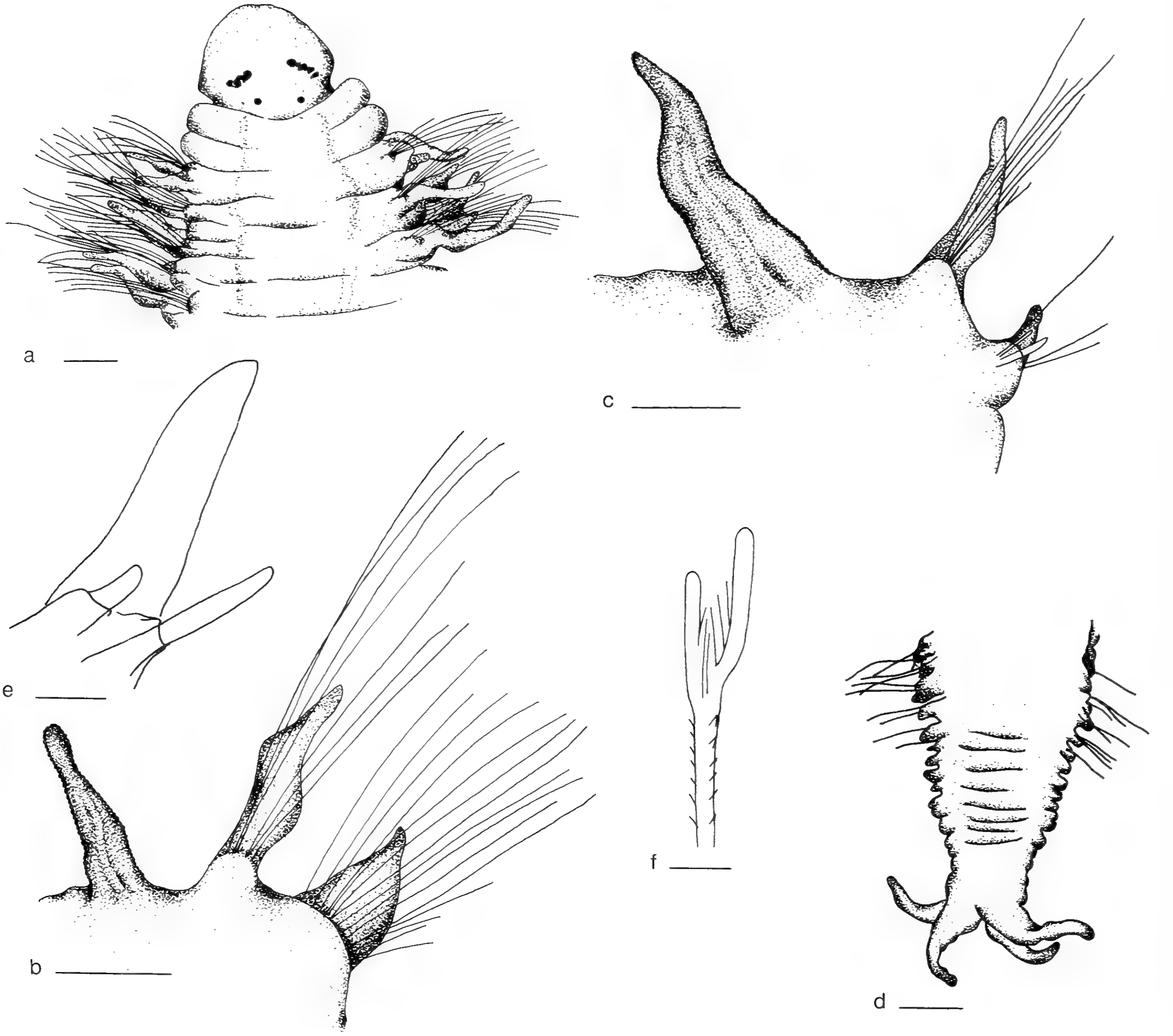

Fig. 7. *Pararicia belizensis*: a, Anterior end, holotype, dorsal view; b, Right parapodium, setiger 8, holotype, anterolateral view; c, Right parapodium, setiger 33, holotype, anterolateral view; d, Posterior end, holotype, dorsal view; e, Abdominal uncini, setiger 33, holotype; f, Furcate notoseta, setiger 9, holotype. Scales: a–d, 100 μm; e, f, 10 μm.

damaged (Fig. 6l) in some specimens. Anal aperture terminal, central; surrounded by about nine papillae (Fig. 6m).

Holotype without tube; some paratypes are covered with fragments of tubes in middle abdominal region. Fragments thin, transparent and covered with sand grains of varying sizes; very small shell fragments and vegetal debris.

Etymology.—The specific name refers to the very distinctive hooks present in this species.

Discussion.—The occurrence of some features is size dependent: The total number of setigers can vary from 32 to 106. The branchiae usually appear at setiger 9 but may be present from setiger 6 to 8. The number of thoracic segments and hence the first appearance of the abdominal hooks, is also size dependent. The variation of these and other characters is summarized in Table 1.

Habitat.—The species is equally well represented both at Twin Cays and Blue Ground Range (Fig. 1), taking the relative sample density into account.

Pararicia, new genus

Diagnosis.—Prostomium rounded, with two to numerous eyes, two asetigerous thoracic segments present; branchiae from one of the thoracic setigers. Notopodial setae include crenulate capillaries and furcate setae. Thoracic neuropodial setae shorter than crenulate capillary setae; thoracic uncini absent. Abdominal neuropodial setae, a few crenulate capillaries in addition to smooth acicular uncini. Four fingerlike anal cirri present.

Etymology.—Derived from the old generic name *Aricia* used in this family.

Type species.—*Pararicia belizensis,* new species.

Pararicia belizensis, new species

Fig. 7

Material examined.—M-3 (one specimen); M-5 (4); M-10 (1); M-11 (one, holotype, USNM 120930, one paratype, USNM 120931); M-12 (2); M-23 (5); M-24 (one paratype, USNM 120939); M-35(1); M-88 (two paratypes, USNM 120953); M-133 (one paratype, USNM 120962); M-135 (1); M-136 (1); M-147 (1).

Description.—Holotype complete with 68 setigers; length 4 mm, greatest width, in thorax, approximately 470 μm, without parapodia. Body slightly more flattened dorsoventrally and wider in thoracic than in abdominal region. Abdomen tapering posteriorly with reduced parapodia in last 15 setigers. Length of other complete specimens from 2 to 9 mm; number of setigers from about 30 to 70. Color as preserved white. Thorax with 10 setigers; abdomen with 58 setigers, including first four transitional setigers.

Prostomium rounded with many eyespots. Two of those are round, clearer and present at the posterior end of the prostomium. The rest are divided in two roughly comma-shaped groups of eyespots at the middle region of the prostomium. No appendages are present (Fig. 7a). In smaller specimens, only two small, round, widely separated eyes are present, near the posterior boundary with the peristomium.

The first two asetigerous segments are distinctly separated from each other and from the prostomium. Mouth about ½ of peristomial width, with lateral lips. Pharynx not everted in any specimens.

Branchiae from setiger 6 in all specimens; becoming reduced in last 15 setigers and absent in last 2–3 setigers; flattened, elongate, triangular, widely separated, never overlapping and recumbent. Mid-abdominal branchiae somewhat larger than other branchiae; otherwise all branchiae similar in size; slightly shorter than notopodial lobes in thorax (Fig. 7b); not deciduous. The last few branchiae are rudimentary and are not visible in the illustration.

All parapodia biramous. Thoracic notopodial postsetal lobes elongate, cirriform, broader in proximal ⅔ of length; slightly increasing in length in first setigers. Thoracic neuropodial postsetal lobes shorter, wider, distally more rounded than corresponding notopodial lobes. Median papillae present; tapering distally (Fig. 7b). Setigers 11 to 14 transitional, characterized by gradual reduction in number of neurosetae and by dorsal shift in neuropodia. Abdominal notopodial postsetal lobes similar to thoracic notopodial postsetal lobes. Abdominal neuropodial postsetal lobes increasingly reduced in length; retaining the same shape (Fig. 7c). Low, dorsal transverse ridges present on abdominal segments.

Both rami with bundles of capillary crenulate setae; thoracic notopodia with about 8–10 setae; thoracic neuropodia with usually 12–18 up to 30 setae; neuropodial fascicles in rows of spreading setae. Notopodial crenulate capillaries longer than neuropodial ones throughout. Uncini absent in thoracic region. Abdominal setigers with reduced numbers of crenulate setae; neuropodia with only four or five setae. Some abdominal notopodia with furcate setae (Fig. 7f). Each abdominal neuropodium with one or two stout hooks. Hooks straight to slightly sigmoid, bluntly pointed, without hoods (Fig. 7e). Small specimens (M-133, M-136, M-147) with hooks from first abdominal setiger. Larger specimens with hooks from the first post-transitional setiger.

Pygidium elongate with four cirriform, distally tapering anal cirri; all anal cirri similar in size. Anal aperture central; terminal (Fig. 7d).

Tubes absent.

Discussion.—The species differs from related taxa as indicated in the discussion of the protoariciin genera.

Etymology.—The specific name refers to the country of origin of the type material.

Habitat.—The species was found mainly in Twin Cays with the exception of M23 and M24 at Blue Ground Range (Fig. 1).

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Appendix 1.—Character-list for protoariciine genera.

1. Prostomial shape
    1. pointed or conical
    2. rounded or truncate
    3. both
2. Branchial start
    0. branchia absent
    1–8. setiger on which branchia begin
3. Shape of branchiae
    0. branchia absent
    1. triangular (flattened)
    2. fusiform
    3. foliaceous
    4. cirriform
4. Anterior and posterior branchiae
    0. all branchiae absent
    1. similar
    2. dissimilar
5. Glandcells in branchial walls
    0. all branchiae absent
    1. present
    2. absent
6. Thoracic furcate notosetae
    1. present
    2. absent
7. Thoracic acicular notosetae
    1. present
    2. absent
8. Thoracic acicular neurosetae
    1. present
    2. absent
9. Thoracic neuropodial subuluncini
    1. present
    2. absent
10. Thoracic neuropodial uncini
    1. present
    2. absent
11. Thoracic notopodial setal lobes
    1. distinct
    2. indistinct
12. Thoracic notopodial postsetal lobes
    1. tapering
    2. fusiform
    3. digitiform (increasing in length through thorax)
13. Thoracic neuropodial postsetal lobes
    1. single
    2. double
14. Thoracic neuropodial postsetal lobes
    1. rounded
    2. tapering
15. Number of transitional segments
    0–7. number of transitional segments
16. Abdominal setal lobes
    1. distinct
    2. indistinct
17. Abdominal neuropodial postsetal lobes
    1. tapering
    2. rounded
18. Abdominal notopodial furcate setae
    1. present
    2. absent
19. Abdominal notopodial acicular setae
    1. present
    2. absent
20. Abdominal neuropodial crenulate setae
    1. present
    2. absent
21. Abdominal neuropodial acicular setae
    1. present
    2. absent
22. Abdominal neuropodial subuluncini
    1. present
    2. absent
23. Abdominal neuropodial uncini
    1. present
    2. absent
24. Abdominal swan-shaped hooks
    1. present
    2. absent
25. Abdominal crested hooks
    1. present
    2. absent
26. Abdominal hooks
    1. of a single kind
    2. of two kinds in vis-a-vis rows
27. Pygidium
    1. with short, blunt projections
    2. with distinct pygidial cirri
28. Number of anal projections or cirri
    0–6. number of anal cirri
29. All anal cirri
    1. similar
    2. of two or more different kinds
30. Eyes
    1. absent
    2. paired
    3. more than a pair
31. Distinct nuchal organs
    1. present
    2. absent

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THREE NEW SPECIES OF *MYZOSTOMA* (MYZOSTOMIDA)

Mark J. Grygier

Abstract.—*Myzostoma armatae,* new species, is an ectocommensal of *Analcidometra armata* (Pourtalès) in the Bahamas and Jamaica, and of *Davidaster discoidea* (Carpenter) in Jamaica. *Myzostoma attenuatum,* new species, is a widespread ectocommensal of diverse Indo-Pacific comatulids. *Myzostoma divisor,* new species, is an Antarctic and sub-Antarctic ectocommensal of *Promachocrinus kerguelensis* Carpenter and of *Notocrinus mortenseni* John. The post-settlement ontogeny of *M. divisor* is documented by scanning electron microscopy.

Myzostoma Leuckart is the largest genus of the Myzostomida, a group of obligately echinoderm-associated worms of unsettled zoological affinities. Currently 115 species of *Myzostoma* are recognized; most of them are ectocommensals of crinoids, although a few form galls on crinoids or infest ophiuroids. The last significant taxonomic paper on this genus was by Jägersten (1940a). My recent work on myzostomes isolated from several major crinoid collections has uncovered many undescribed species. Most of these are represented by few specimens, but the three new species described here are notable for their abundance.

Abbreviations for museums mentioned in the text include: National Museum of Natural History (USNM), British Museum (Natural History) (BMNH), Northern Territory Museum of Arts and Sciences (NTMAS).

Class Myzostomida Graff, 1877
Order Proboscidea Jägersten, 1940b
Family Myzostomatidae Graff, 1884
Genus *Myzostoma* Leuckart, 1836

Myzostoma armatae, new species
Fig. 1

Diagnosis.—Small species with flat, oval body, narrower toward rear, posterior end truncate in uninjured specimens. Marginal zone narrow or poorly evident. About 10 pairs of short marginal cirri, gaps between them larger behind pair 8; supernumerary cirri common. Parapodia acirrate, restricted to anterior 70% of length. Manubrium of parapodial support rods truncate with distal lobes. Lateral organs about halfway from parapodia to margin. Cloacal opening several times farther from margin than proboscis opening. Proboscis unarmed.

Etymology.—Named for the usual host, *Analcidometra armata* (Pourtalès).

History.—McClendon (1907) included one myzostome from *Analcidometra armata* in his type lot of *Myzostoma cerriferoidum,* which otherwise occurred only on *Crinometra brevipinna* (Pourtalès). This type lot has since been pooled (USNM 5780), so the anomalous individual is no longer identifiable, but one very small, damaged specimen 0.90 mm long and 0.86 mm wide might actually be *M. armatae.*

Material.—Five Bahamian samples associated with *Analcidometra armata*: holotype (USNM 118208) and 16 paratypes (USNM 118209) with over 34 crinoids (USNM E17939), 5 Sep 1973, 1 km N350°E of South Bight IV, Goldring Cay, Andros Is., 24°13.9′N, 77°36.2′W, 14–17 m; one paratype (USNM 118210) with two cri-

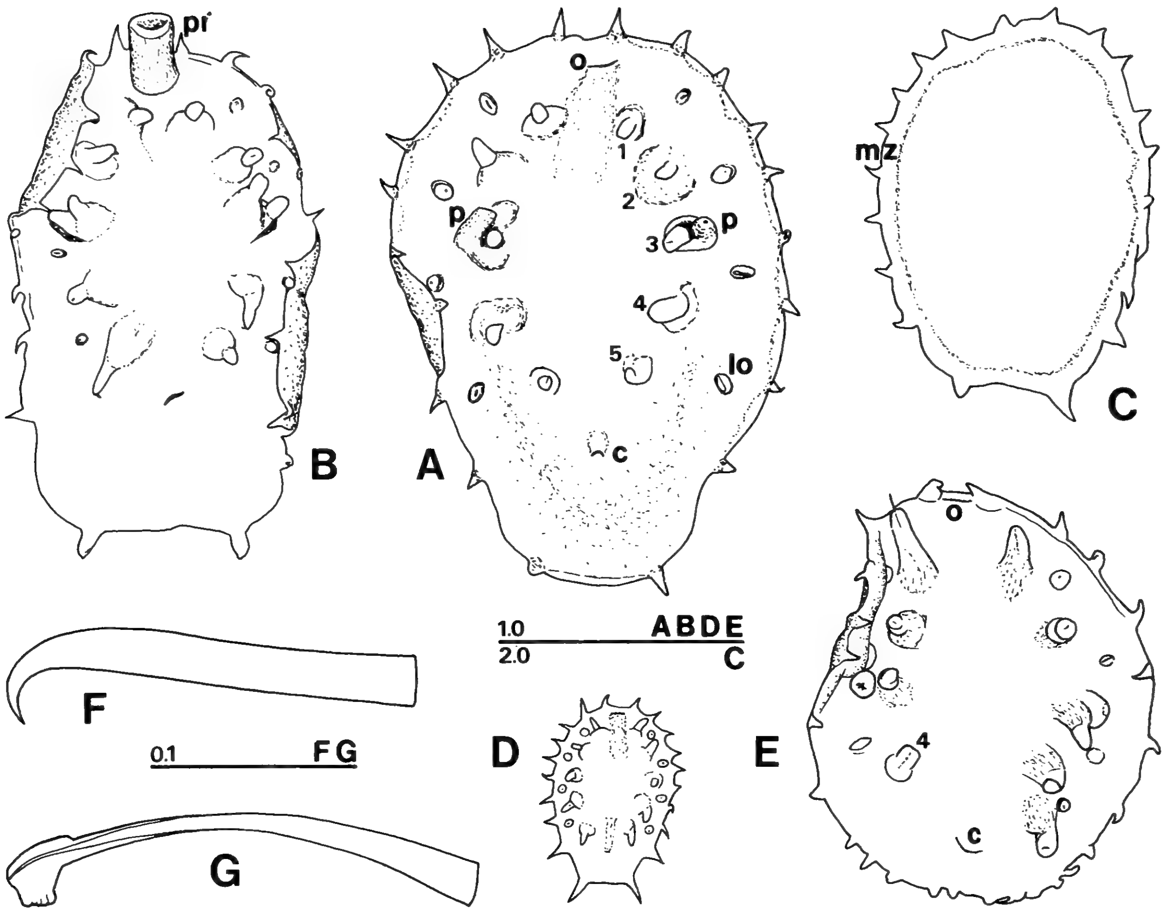

Fig. 1. *Myzostoma armatae.* A, Holotype (USNM 118208), ventral view; B, Paratype from type locality (from USNM 118209), ventral view; C, Large Jamaican paratype (from USNM 118216), dorsal view; D, small Jamaican paratype (from USNM 118220), ventral view; E, Aberrant paratype from type locality, ventral view, missing right parapodium 5 and lateral organ 4, numerous supernumerary cirri on abnormally short and rounded (due to injury?) rear margin of body; F, G, Parapodial hook and support rod, respectively, from a third paratype from type locality. Key: some parapodia numbered from the front in A and E; c, cloacal opening; lo, lateral organ; mz, marginal zone; o, proboscis opening; p, penis; pr, proboscis; scale bars in mm.

noids (USNM E17987), 25 Aug 1973, Marine Farm, Crooked Is., 22°50′N, 73°21′W, 40–52 m; one paratype (USNM 118211) with one crinoid (USNM E17749), 28 Aug 1973, South Long Cay, 22°36.1′N, 74°22.2′W, 15–18 m; six paratypes (USNM 118212) with five crinoids (USNM E17818), 9 Sep 1973, 2 km S118°E of South Bight IV, Goldring Cay, Andros Is., 24°12.4′N, 77°34.9′W, 43 m; 16 paratypes (USNM 118213) with over 20 crinoids (USNM E17951), 9 Sep 1973, same collection as previous entry except 11–12 m.

Seven samples collected by D. B. Macurda, Jr., at Discovery Bay, Jamaica, from *Analcidometra* sp. unless otherwise stated (presumably *A. armata,* since that is the only species currently recognized in the genus; Meyer et al. 1978): 24 paratypes (USNM 118214), W moat and knob in front of Dancing Lady Reef, 9 Jul 1974, 23–27 m; 5 paratypes (USNM 118215), LTS W of Dancing Lady Reef, and Pinnacle II, 10 Jul 1974, 21–27 m; 3 paratypes (USNM 118216), forereef escarpment, Dancing Lady Reef, 8 Jul 1974; 20 paratypes (USNM 118217) on *A. armata,* no detailed collection data; 21 paratypes (USNM 118218), NW edge of forereef terrace, Lynton's Mine, 7 Jul 1974, 21–24 m; 1 paratype (USNM 118219), SE side of Pinnacle I, front of Lynton's Mine, 6 Jul 1974, 24–27 m; 2 paratypes (USNM 118220) on *Davidaster discoidea* (Carpenter), E slope and sand channel E of Lynton's Mine, 9 Jul 1974, 12–17 m.

Description.—Holotype 2.25 mm long, 1.61 mm wide (Fig. 1A). Bahamian paratypes 0.90–2.31 mm long, mean of 16 from

USNM 118213 1.51 mm, of 15 from USNM 118209 1.80 mm, average length : width 1.7–1.8 but range 1.2–2.5 depending on contraction or enrollment. Jamaican paratypes larger (0.73–3.06 mm long, mean of 17 from USNM 118217 2.28 mm), but with same body shape (average length : width 1.7, range 1.2–2.6). Bahamian specimens (Fig. 1A, B, E) uncolored or yellowish, lateral edges of body often downturned; nearly smooth, rather thick cuticle; marginal zone poorly distinguished. Jamaican specimens (Fig. 1C) mostly light brown, sometimes with darker dorsal patches, body usually flat or saddle-shaped, dorsal texture leathery or minutely pebbled; narrow but distinct, translucent marginal zone present.

Following idealized description applies in full to minority of examined specimens; variability described afterwards.

Body oval with rounded front and narrower, often truncate rear, usually with distinct narrowing at level of cloacal opening or of ninth pair of marginal cirri. Fundamentally 10 pairs of marginal cirri, first 8 pairs equally spaced around anterior and lateral margins to level of last parapodia, last 2 pairs progressively father apart, ninth just behind cloacal opening, tenth on rear corners (Fig. 1A–C). In small specimens tenth pair often at least twice as long and thick as other pairs (Fig. 1D), and first pair sometimes also long, but this distinction mostly lost in large specimens. Cirri usually equilaterally or acutely triangular, but longer and thinner in a few specimens of all sizes, or, especially in Jamaican specimens, reduced to little more than marginal thickenings.

Five pairs of parapodia forming oval in anterior two-thirds of ventral side, equally spaced and positioned about halfway from center of oval to anterior and lateral margins, third pair closest to edge (Fig. 1A, B, D). Parapodia small, with conical, acirrate base and stubby, finger-like distal part; latter extensible enough to overreach body margin, even in rear parapodia (only retracted ones illustrated). Parapodial hooks moderately stout, nearly straight, tips evenly rounded and tapered, bending more than 90° (Fig. 1F). Support rods thinner and a little longer than hooks, manubrium expanded very little on rear side, front side truncate about 5 small, distal lobes (Fig. 1G). One or 2 replacement hooks present. Penes present as short, broad, cylindrical nozzles arising from lateral bases of third parapodia and sometimes reaching as far as body margin, diameter greater than that of distal part of parapodium (Fig. 1A, B, E). Four pairs of lateral organs alternating with parapodia and forming arcs parallel to body margin about halfway between parapodia and margin (Fig. 1A); lateral organs small, round or more usually radially oval, resembling short, cylindrical tubes when protruded. Proboscis opening ventral, about one-third of way from front margin to first parapodia; extended proboscis cylindrical, twice as long as thick, lacking papillae (Fig. 1B). Cloacal opening at level of ring of lateral organs, much closer to last parapodia than to rear body margin.

Variability.—Body outline and marginal cirri subject to much variability, apparently due to injury from predators; lateral edges and more often rear end often showing evidence of healing of large wounds and sometimes missing parapodia (Fig. 1E). Rear often deeply notched on right or left side, sometimes entire postanal region missing. In a few cases, rear split lengthwise. Ten marginal cirri on each side of body in only 30% of 70 specimens from 4 lots, unilateral cirral count 4–21, but 8–12 86% of the time. Low cirral counts due to injury except in a few apparently undamaged Jamaican specimens simply lacking cirri towards rear. Commonly from one to two supernumerary cirri of usual form. If more cirri present, extra ones most often found in healed posterior areas, less often laterally (Fig. 1E); such cirri smaller than normal and generally appearing in closely spaced rows.

Remarks.—Of described Caribbean myzostomes, only *Myzostoma rotundum* Graff, 1883, has an oval body with an eccentric ring of parapodia (Graff 1884). The body form and size (1.7 × 1 mm), the small parapodia excluded from the rear part of the body, and the position of the proboscis opening match *M. armatae.* But the wide marginal zone of *M. rotundum* (⅙ of body diameter), and its much larger hemispherical lateral organs that are very close to the margin (in the marginal zone itself), are different. So are the high number (22 along one side of the body), equal spacing, and rather filiform shape of its marginal cirri and the wider spacing of the parapodia towards the rear.

Except for two specimens found with *Davidaster discoidea, Myzostoma armatae* seems to be restricted to *Analcidometra* (presumably always *A. armata*) as a host, and this new species is currently known from the Bahamas and Jamaica at 12–52 m. The specimens from *D. discoidea* co-occurred with another undescribed species of *Myzostoma.*

Myzostoma attenuatum, new species
Fig. 2

Diagnosis.—Body elongate, up to 4.5 mm long, with tapered, postanal, caudal region in undamaged specimens. No translucent marginal zone. Numerous short, irregularly sized, closely spaced marginal cirri back to level of cloacal opening, sparser in caudal region. Parapodia acirrate, usually confined to front half of body, a little closer to margin than midline. Parapodial hooks very thick, manubrium of support rods hatchet-shaped. Round lateral organs halfway from parapodia to margin, half parapodial diameter when protruded. Proboscis opening closer to first parapodia than margin, proboscis unarmed.

Etymology.—Named for the drawn out, attenuated caudal region of undamaged specimens.

Type material.—Unless otherwise specified, all specimens loose in jars with supposed hosts. Holotype (USNM 118221) with one *Capillaster sentosa* (Carpenter) (USNM 34844), Albatross stn. 5146, 5.7 km SE of E Sulade Is., near Siasi, Sulu Archipelago, Philippines, 5°46′40″N, 120°48′50″E, 44 m, 16 Feb 1908; 2 paratypes (USNM 118222) with 3 *Comaster multifida* (J. Müller) (USNM E34538), collected by D. L. Meyer, Lizard Is., Queensland, Australia; 3 paratypes (USNM 118223) with 2 *Colobometra perspinosa* (Carpenter) (USNM E34765), collected by D. L. Meyer, E side of Ta Bui Is., Indonesia, 6–18 m, 29 Mar 1975; 10 paratypes (USNM 118224) with 2 *Oxymetra finschi* (Hartlaub) (USNM E34861), collected by D. L. Meyer, Malaysia; 20 paratypes (USNM 118225) with 2 *O. finschi* (USNM E34576), collected by D. L. Meyer, Singapore; 1 paratype (USNM 118226) found halfway out along arm of *Pontiometra andersoni* Carpenter (USNM 35222), same collection as holotype; 3 paratypes (USNM 118227) with 1 *P. andersoni* (USNM E3130), New Harbour, Singapore, 1899; 9 paratypes (USNM 118228) with 2 *Pontiometra* sp. (USNM G2605), collected by D. L. Meyer, Lizard Is., Queensland, Australia, 1975; 1 paratype (USNM 118229) with 2 *Decametra mylitta* A. H. Clark (USNM E11628), International Indian Ocean Expedition, R/V *Anton Bruun* cr. 1, stn. 47B, northern Bay of Bengal, 19°50′N, 92°55′E, 22–30 m, 5 Apr 1963; 10 paratypes (NTMAS Ref. no. W326), collected from *Cenometra cornuta* A. H. Clark by R. Lockyer, Cootamundra Shoal, Timor Sea, Northern Territory, Australia, stn. 2/43, 10°50′S, 129°13′E, 20 m, 10 May 1982; 1 paratype (author's collection), host unknown, collected by A. Pietsch, Maldives, 1985.

Additional material.—3 partial specimens (USNM 118230) with *Stephanometra oxyacantha* (Hartlaub) (USNM E34854), collected by D. L. Meyer, Singapore; 1 specimen (USNM 118231) with 1 *Comaster gracilis* (Hartlaub) (USNM E35356), collected by D. L. Meyer, Lizard Is., Queens-

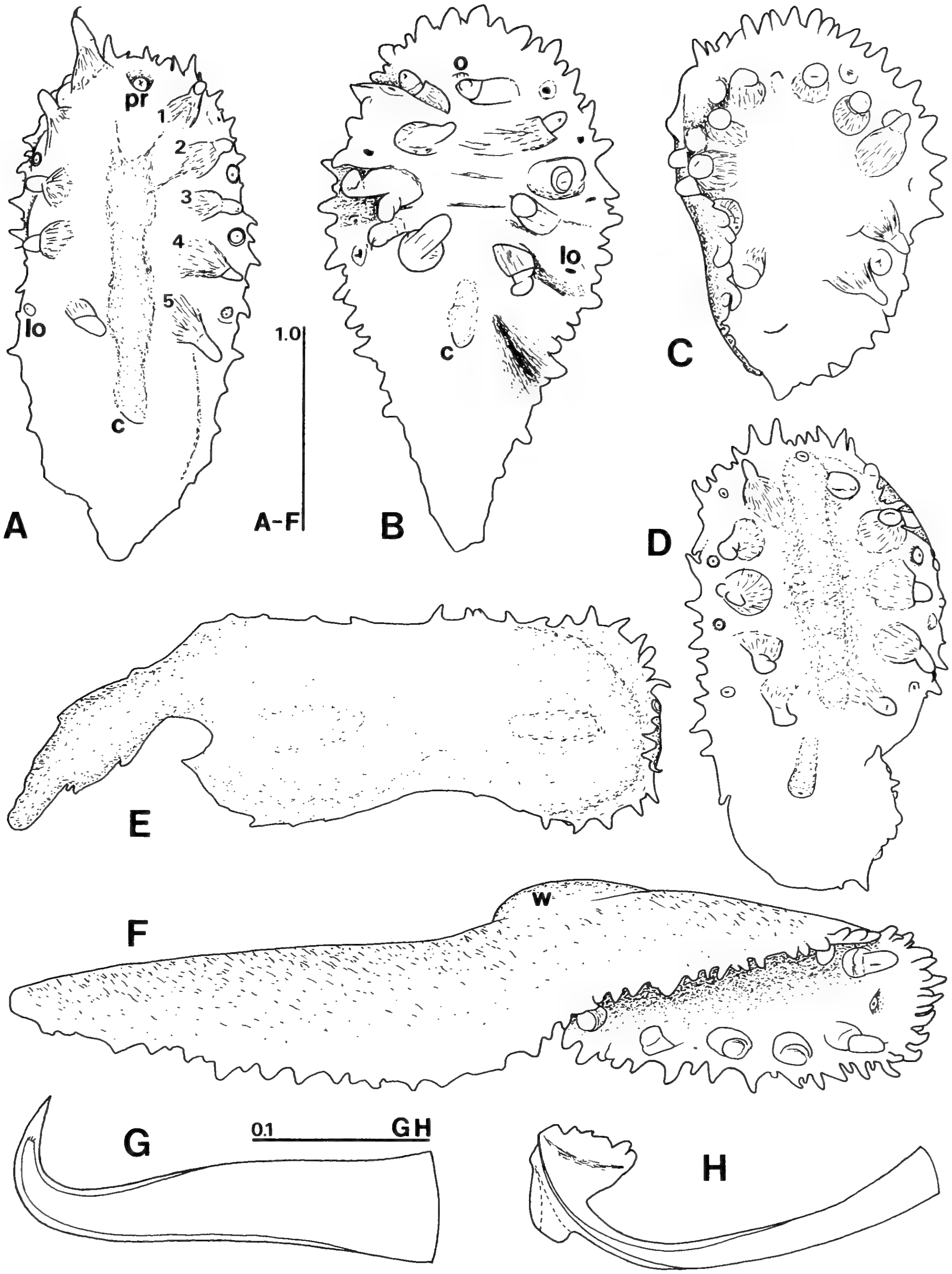

Fig. 2. *Myzostoma attenuatum.* A, Holotype (USNM 118221), ventral view, some lateral organs not visible due to upturned body margin; B, Paratype, ventral view (personal collection); C, Unusually short paratype (from USNM 118228), ventral view; D, Posterolaterally injured paratype (from USNM 118227), ventral view; E, Paratype (from USNM 118225) showing abnormal development of caudal part of body, presumably due to injury, dorsal view; F, Longest paratype (from USNM 118223), body twisted, lateral organs not shown; G, H, Parapodial hook and support rod, respectively, from specimen in same lot as C. Key: as in Fig. 1, except w, lump apparently caused by endoparasitic worm; scale bars in mm.

land, Australia; 1 specimen (USNM 118232), host unknown, from International Indian Ocean Expedition, R/V *Anton Bruun* cr. 1, stn. 47B (details above); 15 specimens (USNM 118233), host unknown, from International Indian Ocean Expedition, R/V *Anton Bruun* cr. 1, stn. 18A, Andaman Sea off Phuket, Thailand, 7°34′N, 98°00′E, 77 m, 21 Mar 1963; 1 damaged specimen (NTMAS W325), collected from *Petasometra helianthoides* A. H. Clark, same collection data as NTMAS W326 above except stn. 2/50.

Description.—Body usually elongate and posteriorly tapered (Fig. 2A, B, F), but subject to injury-induced malformations (Fig. 2D, E). Front half either convex dorsally and concave ventrally with downturned margins or slightly convex dorsally and flat ventrally, with parallel, extended lateral margins. Dorsum smooth, fine-textured, sometimes with low, longitudinal ridge over proboscis and gut. Color usually dark brown, but poorly preserved specimens colorless or with dark dorsal speckling. No marginal zone. Holotype 2.50 mm long, 1.11 mm wide, with upturned sides (Fig. 2A), other undamaged specimens 0.88–4.46 mm long, length : width from 1.6–3.5 (all measurements excluding cirri). Marginal cirri very numerous and closely spaced anterior of level of cloacal opening (about 40 in holotype, varying widely from about 25 to nearly 50 in other specimens), caudal part of body lined by smaller and more widely spaced cirri. Cirri bluntly triangular to digitiform with 3-fold difference in length and thickness in a single specimen. Alternating size pattern seen in many specimens (Fig. 2A). Caudal region usually symmetrical, but in many specimens secondarily shortened (Fig. 2C), or split longitudinally due to injury (predation?). Entire caudal region sometimes lost or bizarrely asymmetrical (Fig. 2E).

In undamaged specimens, five pairs of parapodia arranged in two nearly parallel rows or shallow arcs on anterior half or one-third of ventral side, slightly closer to margin than to midline (Fig. 2A–D, F). Obliquely conical base of parapodium lacking medial cirrus; distal part of parapodium a stubby, rounded process up to twice as long as thick. Parapodial hooks very stout, evenly tapered, tip bent at 90° (Fig. 2G). Support rods of same length but much thinner than hooks, manubrium hatchet-shaped, produced on both front and rear sides (Fig. 2H). Two replacement hooks. Pair of penes laterally on swollen basal parts of third parapodia (Fig. 2B, D), thicker than distal part of parapodium when protruded. Four pairs of lateral organs alternating with parapodia halfway between them and margin; when withdrawn, minute apertures surrounded by slightly raised annuli (Fig. 2B, C); expanded lateral organs with wide aperture and more prominent annulus, diameter about half that of distal part of parapodium (Fig. 2A, D). Proboscis opening ventral, closer to first parapodia than to anterior margin, proboscis cylindrical, slightly tapering, unarmed (tip visible in Fig. 2A, F). Cloacal opening a little farther posterior of fifth parapodia than latter from fourth pair.

Longest specimen with oval dorsal hump presumably indicating presence of internal parasite (Fig. 2F). Injured specimens sometimes lacking one or two parapodia on one or both sides.

Remarks.—*Myzostoma attenuatum* resembles two described species, *M. dentatum* Graff, 1884, and *M. moebianum* Graff, 1884. The first of these was described on the basis of one specimen, which has not been located, from the Torres Straits (Graff 1884). A second specimen of *M. dentatum,* which also has not been located, was found in a jar with seven species of Moluccan crinoids (Graff 1887). The elongate, oval body and supernumerary marginal cirri recall *M. attenuatum,* but *M. dentatum* has a wide, distinct marginal zone, the proboscis opening closer to the front margin, the parapodia closer to the midline and not particularly confined to the front half of the body, and a rounded, untapered rear.

Myzostoma moebianum, a species described on the basis of collector's notes and nearly useless microscopical preparations, is from an unknown host at Fouquet Is. southeast of Mauritius (Graff 1884). Its body outline and parapodial placement are similar to small specimens of *M. attenuatum*; the rear is tapered and the parapodia, with very thin support rods, are restricted to the anterior two-thirds. It differs from the present species in having untapered parapodial hooks, somewhat differently shaped support rod manubria, and most importantly a pair of lateral organs behind the fifth pair of parapodia. This last feature is unusual, otherwise occurring only in *M. costatum* sensu Boulenger (1913a), and given the unorthodox way the original description was prepared, it might be a mistake. If this could be proved, then *M. attenuatum* might be a synonym of *M. moebianum*.

Myzostoma attenuatum shows little host specificity. It infests 10 species of oligophreatan comatulids that belong to two superfamilies, three families (Comasteridae, Mariametridae, Colobometridae), and nine genera, one of the widest host ranges of the myzostomes I have investigated. Geographically it ranges from the Maldives and the Bay of Bengal east through Singapore, Malaysia, and Indonesia to the southern Philippines and northern Australia, and its recorded depth range is 6–30 m. The holotype co-occurred with *M. furcatum* Graff, 1887, and *M. longimanum* (Jägersten, 1937); USNM 118222 with *M. furcatum* and *M. ambiguum* Graff, 1887; and USNM 118226 with *M.* sp. cf. *triste* Graff, 1877.

Myzostoma divisor, new species

Figs. 3, 4

Diagnosis.—Body a round disc with posterior pair of cylindrical caudal processes up to 1.75 times longer than body diameter. Nine pairs of moderately long, equal cirri around disc, additional pair at ends of caudal processes. Parapodia two-thirds of way from center of disc to margin, basal part with pointed medial cirrus, distal part in two sections, extremely extensible. Parapodial hooks and support rods very long and slender, manubrium of latter digitiform. Four pairs of relatively large, round lateral organs abutting margin. Proboscis opening terminal, proboscis unarmed. Cloacal opening terminal, on papilla between caudal processes.

Etymology.—From Latin *divisor,* a divider, since larger animals in dorsal view resemble a pair of dividers.

Type material.—Holotype (BMNH ZB 1980.460) and 12 paratypes (BMNH ZB 1980.461–472) from pinnules of *Promachocrinus kerguelensis* Carpenter, Discovery stn. 1652, 75°56.2′S, 178°35.5′W, 567 m, 23-I-1936. 3 lots collected by W. H. Littlewood, Deep Freeze II, R/V *Staten Island,* hosts unknown: 1 paratype (USNM 118234), Weddell Sea, 77°32′S, 44°45′W, 284 m, 21-I-1957; 1 paratype (USNM 118235), stn. 24, 77°21′S, 44°30′W, 300 m, 20-I-1957; 5 paratypes including 2 early juveniles (USNM 118236), Weddell Sea, 75°27′S, 57°12′W, 549 m, 17-I-1957. 1 paratype (USNM 118237), host unknown, *Hero* cr. 824, stn. 4-1, 65°13.60–13.67′S, 64°14.72–15.07′W, 49–58 m, 16-III-1982; 7 paratypes (USNM 118238), host unknown, *Hero* cr. 691, stn. 2A, 64°49.5′S, 63°47′W, 70 m, 1-II-1969; 107 intact, 272 damaged, and 26 early juvenile paratypes (USNM 118239), some used for SEM, host unknown, *Hero* cr. 824, stn. 26-1, 64°14.30–13.80′S, 61°57.60–58.30′W, 238–285 m, 24-III-1982.

Additional material.—One specimen (BMNH ZB 1980.540) from pinnules of *P. kerguelensis,* Discovery stn. 1658, off Franklin Is., 76°9.6′S, 168°40′E, 520 m, 26-I-1936; one specimen (BMNH ZB 1980.547) from genital pinnules of female *Notocrinus mortenseni* John, Discovery stn. 187, NeuMayr Channel, Palmer Archipelago, 64°48′30″S, 63°31′30″W, 259–354 m, 18-III-1927; five specimens (BMNH ZB 1980.543–546) from pinnules of *P. kerguelensis,* Discovery stn. 156, 53°51′00″S, 36°21′30″W, 200–236 m, 20-I-1927; two specimens (BMNH ZB 1980.541–542) free on lower parts of arms of *P. kerguelensis,* Discovery stn. 42, off mouth of Cumberland

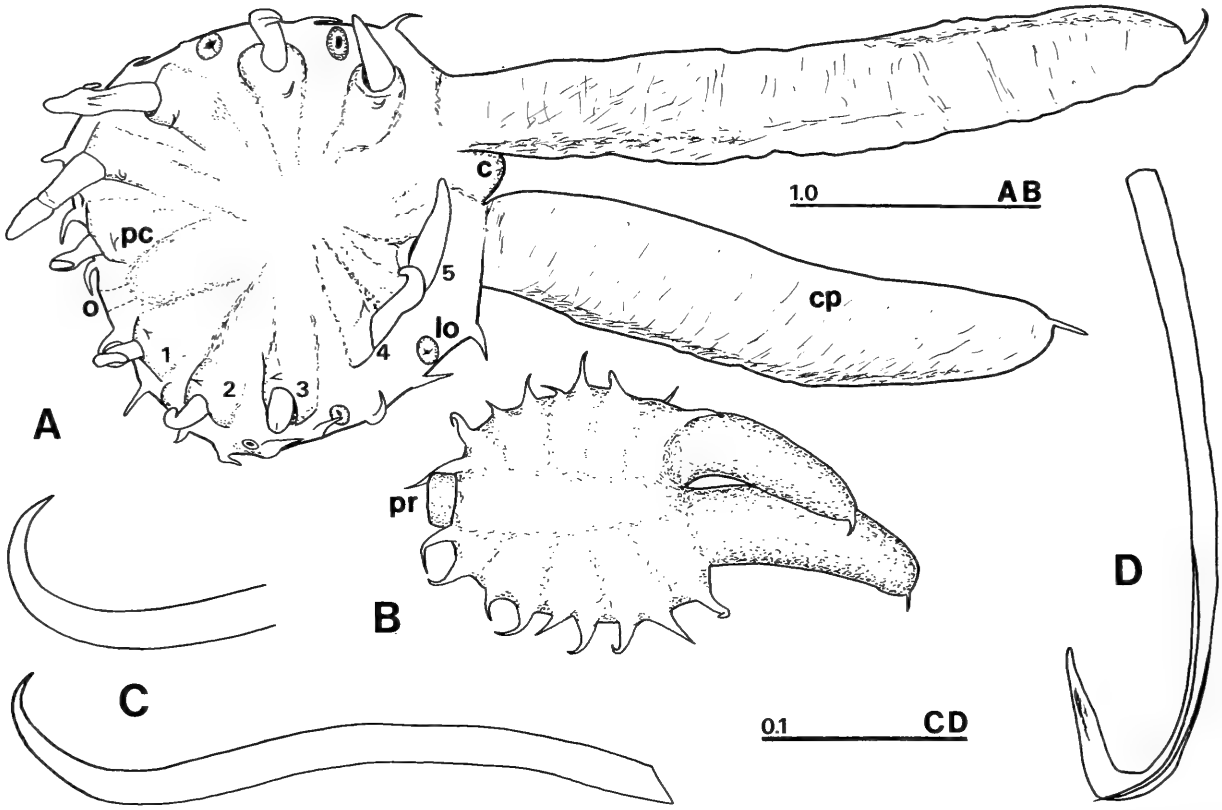

Fig. 3. *Myzostoma divisor.* A, Holotype (BMNH ZB 1980.460), ventral view; B, Paratype from type locality (from BMNH ZB 1980.461–472), dorsal view; C, Parapodial hook and distal part of another from paratype (from USNM 118239); D, Parapodial support rod from same specimen as C. Key: as in Fig. 1, except cp, caudal process; pc, parapodial cirrus; scale bars in mm.

Bay, South Georgia, 10.5 km N89°E of Jason Lt. to 6.7 km N39°E, 120–204 m, 1-IV-1926; two specimens (USNM 118240), host unknown but one specimen from gorgonian washings, *Hero* cr. 824, stn. 14-1, 64°48.63–48.20'S, 64°4.00'W, 70–150 m, 19-III-1982; one specimen (USNM 118241) from crinoid washings, *Hero* cr. 824, stn. 26-1, 64°14.30–13.80'S, 61°57.60–58.30'W, 238–285 m, 24-III-1982.

Description of adults.—Body a round, flat disc with pair of cylindrical caudal processes and nine pairs of marginal cirri. Specimens from type locality larger than others. Holotype disc diameter 1.79 mm, right and left caudal processes (omitting terminal cirri) 2.44 and 3.12 mm long, respectively (Fig. 3A). Largest paratype with disc diameter 2.12 mm, longer caudal process 2.82 mm. Maximum ratio of caudal process length to disc diameter 1.75 in specimen 1.10 mm across; caudal processes generally, but with many exceptions, relatively longer in larger individuals (Fig. 4; see ontogeny section below).

Color yellowish brown, no translucent marginal zone. Dorsum smooth or with longitudinal swelling, and sometimes with radial grooves between parapodial muscle masses (Fig. 3B). Nine pairs of evenly spaced, equally long marginal cirri, similar pair at ends of caudal processes, though these often broken off; in holotype marginal cirri about 0.14 mm long, terminal ones on caudal processes about 0.16 mm long. Caudal processes cylindrical or somewhat flattened dorsoventrally, diameter about one-fifth that of body disc (Fig. 3A, B).

Five pairs of parapodia equally spaced in arcs at least two-thirds of way from center of body disc to margin, members of first pair and especially fifth pair widely separated compared to spacing within arcs (Figs. 3A, 4C, D). Basal part of parapodium an

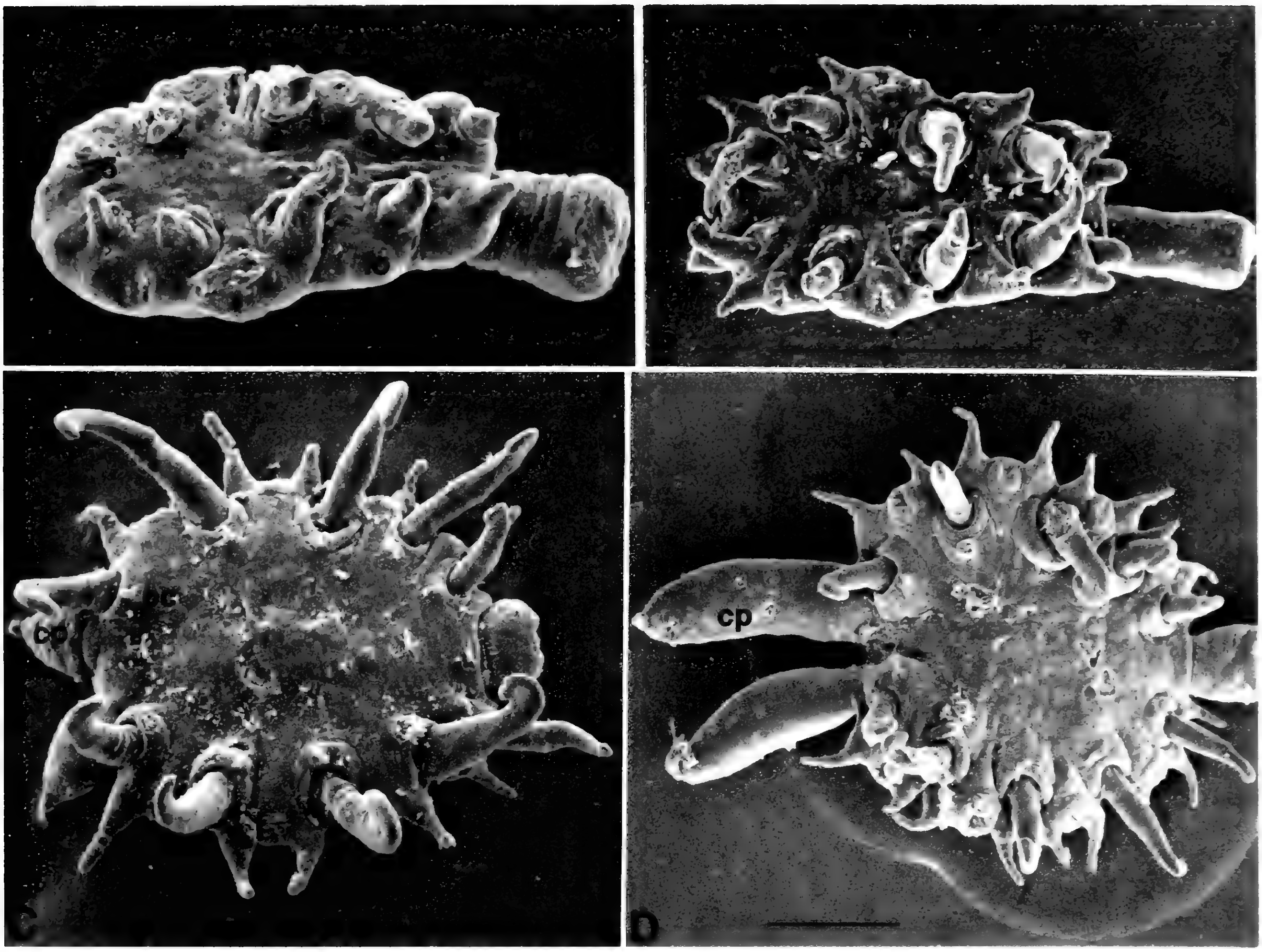

Fig. 4. *Myzostoma divisor.* A–D, Successively later stages in early, post-settlement ontogeny, scanning electron micrographs of paratypes (from USNM 118239). Key: as in Fig. 1 except mc, marginal cirrus; cp, caudal process; pc, parapodial cirrus; scale bars 0.2 mm.

obliquely truncate, radially inclined cylinder with slender cirrus near apex of medial side (Figs. 3A, 4D). Long, slender, apparently bipartite distal part of parapodium projecting radially, either straight or medially curved, extremely extensible and capable of doubling length. Parapodial hooks long, slender, weakly sigmoid, tips exhibiting range of curvatures (Fig. 3C), apparently most broadly rounded in third pair (cf. Fig. 4A). Support rods same length, slightly thinner than hooks, manubrium a long, digitiform process (Fig. 3D). One or two replacement hooks. Penes present as small buttons at lateral bases of third parapodia. Four pairs of lateral organs alternating with parapodia, outer edges nearly or actually abutting body margin, inner edges just inside outer edges of parapodial bases (Figs. 3A, 4B). Lateral organs round, with same or greater diameter as distal parts of parapodia, low mounds with radially elongate, stellate apertures when retracted, round pads with depressed centers when protruded. Proboscis opening on anterior margin, proboscis a short, unarmed cylinder almost as thick as caudal processes (Figs. 3B, 4D). Large cloacal papilla on rear margin of body between bases of caudal processes (Fig. 3A).

Ontogeny.—Seven minute to small paratypes from USNM 118239 were examined by SEM (Fig. 4) after critical point drying and sputter coating with carbon and gold.

Earliest stage (Fig. 4A) with oval body 200 μm long not counting proboscis, widest behind third parapodia, tapering more towards front than rear. No marginal cirri or caudal processes developed. Third parapodia largest, others smaller towards front and rear, last pair much smaller than first, no parapodial cirri present. Lateral organ apertures small, on sides of body. Apparently non-retractile proboscis 60–80 μm long. Cloacal opening not seen (nor in any other SEM specimen).

Next stage (Fig. 4B) represented by specimen 430 μm long (310 μm of main body plus extended proboscis); body 0.21 mm wide at level of third pair of lateral organs. Most marginal cirri present as blunt, tapered processes, last pair (caudal process rudiments) thicker than others. Articulation groove between basal and distal part of parapodium deeper and more nearly circular than in preceding stage, parapodial cirri now clearly present. First pair of parapodia much smaller than other 4 pairs. Lateral organs visible as raised annuli around small pores.

In later stages (Fig. 4C, D) body round, marginal cirri and distal parts of parapodia elongate. Caudal processes first thickened into cones as long as marginal cirri (Fig. 4C); illustrated specimen the smallest of its type, wider but slightly shorter than specimen in Fig. 4B. Caudal processes becoming elongate (Fig. 4D) and proboscis retractable.

Remarks.—The only described species similar to *M. divisor* are *M. bicaudatum* Graff, 1883, and the species described under the name *M. filicauda* by Graff (1884). *Myzostoma bicaudatum* was collected in the Gulf of Mexico, and the unique specimen, which has been lost, was most fully described by Graff (1884). It has a round body 0.45 mm across with a pair of caudal processes. However, there are 10 pairs of marginal cirri, not 9, the front and rear cirri are considerably longer than the lateral ones, the caudal processes lack a "terminal thread" (=terminal cirrus), and the proboscis opening is ventral; no parapodial cirri are reported, but in such a small animal they may have been overlooked.

Myzostoma filicauda was most fully described by Graff (1884) from specimens collected by the *Corvin* off Sandkey; these specimens have also been lost. Graff (1883, 1884) has accidentally caused a nomenclatural confusion between this species and *M. filiferum* Graff, 1884 (from the Torres Straits), because his 1883 original diagnosis of *M. filicauda* agrees with the 1884 description only in terms of size and host, while the characterization of the caudal processes fits the 1884 original description of *M. filiferum* (terminal threads longer than body diameter). Since the type specimen of the latter species is also missing, it is now impossible to resolve this apparent lapsus of Graff's, so I assume that Graff's actual conceptions of the two species are those presented in the *Challenger* Report (Graff 1884), from which the 1883 paper was abstracted. *Myzostoma filicauda,* as here understood, differs from *M. divisor* in having 10 pairs of marginal cirri as well as the pair on the caudal processes, and the lateral cirri are distinctly shorter than the anterior and posterior ones. The proboscis may have papillae, although the latter may be folds in the wall of the proboscis opening, to judge from the illustration. *M. filicauda* also has large, radially oval, lateral organs instead of round ones. Finally, it is hard to imagine that a single species of myzostome could range from Antarctica to the subtropical and tropical shallows of the Atlantic or Pacific.

Few studies of myzostome post-settlement ontogeny have been conducted. Jägersten (1940b) has given the most complete account, based on *Myzostoma cirriferum* Leuckart, 1836, and Kato (1952) studied a species identified as *M. ambiguum* Graff, 1887; both authors reviewed the scanty literature. The earliest observed stage in *M. divisor* corresponds to Jägersten's (1940b) fig. 4 of *M. cirriferum* and fig. 7 of *M. alatum* Graff, 1884, and Kato's (1952) fig. 41 of *M. ambiguum* in having an oval body, all 5 pairs of parapodia developed, the proboscis unretracted, and no marginal cirri. There are no obvious identifying features at this stage, and the present minute juveniles are identified as *M. divisor* on the basis of their association with hundreds of older, positively identifiable specimens. In *M. cirriferum* the first pair of parapodia is apparently the last to arise; in *M. ambiguum* the first and last pairs appear after the middle three. The first pair is small compared to the middle three pairs in the present juveniles, but in the youngest ones the sixth pair is even smaller, suggesting that it may have appeared last, and the first pair second to last. The progressive envelopment of the proboscis (actually the anterior part of the body; Jägersten 1940b) by the larger posterior part of the body is well exhibited by *M. divisor.*

Until now, only three species of myzostomes have been reported from Antarctic waters, one each of *Myzostoma* (*M. antarcticum* Stummer-Traunfels, 1908), *Cystimyzostomum* (*C. cysticolum* Graff, 1883), and an unnamed *Asteromyzostomum* (cf. Stummer-Traunfels 1908, Boulenger 1913b, Grygier 1988). Of these, only *C. cysticolum* is known from *Promachocrinus kerguelensis,* where it occupies soft cysts on the oral disc, and none are known from *M. divisor*'s other identified host, *Notocrinus mortenseni. Promachocrinus* and *Notocrinus* belong to different suborders of the Comatulida, so *M. divisor* is probably not at all host specific. Its currently known geographical and depth range includes the Ross Sea, Weddell Sea, waters northwest of the Antarctic Peninsula, and South Georgia, at 49–567 m.

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SYSTEMATIC STATUS OF *LEPIDOTEUTHIS, PHOLIDOTEUTHIS,* AND *TETRONYCHOTEUTHIS* (CEPHALOPODA: OEGOPSIDA)

Clyde F. E. Roper and C. C. Lu

Abstract.—The status of the nomenclature and systematics at species, generic, and familial levels for *Lepidoteuthis, Pholidoteuthis,* and *Tetronychoteuthis* is reviewed and current knowledge consolidated based on examination of specimens and analysis of literature.

The systematics and nomenclature of the squid genera *Lepidoteuthis* Joubin, 1895, *Pholidoteuthis* Adam, 1950, and *Tetronychoteuthis* Pfeffer, 1900 have become so confused that it is difficult to discuss any of the species without raising doubts concerning the entities involved. During the course of a study of the comparative functional morphology of dermal structures in several species of oceanic squids (Roper & Lu 1989), we were able to make some conclusions about relationships in this group. We present here the results of our examination of numerous specimens and the literature in an effort to clarify the situation.

Tetronychoteuthis had been placed for "convenience" in the Lepidoteuthidae with *Lepidoteuthis* and *Pholidoteuthis* (Roper et al. 1969, Voss 1977) because of their common character of dermal "scales," but the actual relationships of these genera have remained obscure because of a lack of specimens to support research. Clarke (1980) and Clarke & Trueman (1988) separated these genera into the monotypic family Lepidoteuthidae (*Lepidoteuthis grimaldii* Joubin, 1895) and the family Pholidoteuthidae, containing *Pholidoteuthis boschmai* Adam, 1950, *P. adami* Voss, 1956, and *Tetronychoteuthis massyae* Pfeffer, 1912. The status of *Tetronychoteuthis dussumieri* (Orbigny) sensu Pfeffer, 1900, in relation to *Onychoteuthis dussumieri* Orbigny, 1839, needs clarification.

Our review suggests that the following situations exist.

1) *Onychoteuthis dussumieri* (Orbigny, 1839 [in 1834–1848] (p. 335, *Onychoteuthis* pl. 13, figs. 1–6; type locality—Mauritius; type depository—Museum National d'Histoire naturelle, Paris?) is a species of *Moroteuthis* Verrill, 1881, based on the presence of two rows of hooks on the tentacular clubs, the dermal structures that are larger and fewer than in *Tetronychoteuthis massyae* Pfeffer, 1912 (pp. 102–104, pl. 14, figs. 15–19), smooth sucker rings on the arm suckers, and an onychoteuthid shape of the gladius, fins and body. Therefore, this species belongs in the family Onychoteuthidae and bears the name *Moroteuthis dussumieri* (Orbigny, 1839 [in 1834–1848]). Furthermore, future research may show it to be a senior synonym of a currently recognized species of *Moroteuthis* Verrill, 1881.

2) The specimen that Pfeffer (1900) referred to *Tetronychoteuthis dussumieri* (Orbigny, 1839) when he established the genus cannot be conspecific with Orbigny's species because it has no hooks on the tentacular clubs and has a gladius very different from that of *O. dussumieri* Orbigny (see Pfeffer, 1912:98–102, pl. 13, figs. 1–3, pl. 14, figs. 10–14). Furthermore, it is so different from any onychoteuthid that it belongs to a different genus and family as well. Pfeffer's specimen, therefore, is a misidentification of the type species of his genus *Tetronycho-*

teuthis. So, what is the type species of *Tetronychoteuthis* - the real *dussumieri* of Orbigny or the species that Pfeffer actually had in hand? The case must be referred to the International Commission on Zoological Nomenclature for a decision under Article 70 of the International Code. In such cases, the Commission usually makes a decision based on subsequent usage of the names, with present opinion and usage of active workers weighing heavily (pers. comm., F. M. Bayer). Toll's (1982:247) placement of "*T. dussumieri*" of Pfeffer into the synonymy of *Pholidoteuthis boschmai* Adam, 1950 is premature from the standpoint of the Code (ICZN 1985).

Rees and Clarke (1963:853–854, fig. 1) recorded as *T. dussumieri* (Orbigny) five specimens from the Northwest Atlantic Ocean. We point out for the record that this is a misidentification and that the specimen in the photograph is a *Brachioteuthis* sp. Presumably the other four specimens were *Brachioteuthis* as well.

3) *Pholidoteuthis boschmai* Adam, 1950 (pp. 1592–1598, pls. 1–3, figs. 1–6; type locality—Flores Sea; type depository—Rijksmuseum van Natuurlijke Historie, Leiden) was erected as the type species of a new genus *Pholidoteuthis* and new family, Pholidoteuthidae. It bears "hinged" suckers and no hooks on the tentacular club. The gladius, the dermal structures (Roper and Lu 1989) and the club structure of *P. boschmai* are similar to those of Pfeffer's "*T. dussumieri*," and Adam (1950), Clarke (1980: 129–138, pl. II, figs. 1, 2, text-fig. 94), and Toll (1982:247–252, pl. 28C) suggested that these two taxa are conspecific. We, however, feel that currently there is insufficient information about Pfeffer's species to verify this assertion. If examinations of Pfeffer's specimen of "*dussumieri*" and Adam's type of *boschmai* proves them to be conspecific, the correct generic and specific names will have to be determined by a submission to the International Commission on Zoological Nomenclature (see 2 above).

4) *Pholidoteuthis adami* Voss, 1956 (pp. 132–136, fig. 9; type locality—Gulf of Mexico; type depository—National Museum of Natural History, Washington) shows close familial affinity to *Lepidoteuthis grimaldii* Joubin, 1895 (pp. 1172–1173, 1 fig.; type locality—Azores Islands; type depository—l'Institut Oceanography, Monaco) in the structure of the dermal cushions (formerly called "scales"; see Roper & Lu 1989), the gladius and the shape, conformity, and consistency of the mantle and fins. Therefore, we recommend that *P. adami* Voss, 1956 be placed in the family Lepidoteuthidae.

However, the correct generic designation cannot be determined until the status of *P. boschmai,* the type of the genus, is established. Nor do we know if *adami* and *boschmai* are, in fact, congeneric. Toll (1982:250–251) demonstrated that the gladius of *P. adami* (and *L. grimaldii*) is so different from *P. boschmai* that a congeneric relationship of currently aligned *Pholidoteuthis* species appears untenable.

5) *Tetronychoteuthis massyae* Pfeffer, 1912 (pp. 102–104, pl. 14, figs. 15–19; type locality—48°N15°W (Atlantic); type depository—unknown). This species has to be retained in the genus *Tetronychoteuthis* until the nomenclatural status of "*T. dussumieri*" of Pfeffer (1900) is resolved (see 2 above) and the relationship between the two species is established. Several authors (Pfeffer 1912; Clarke 1966, 1980; Rancurel 1970) have suggested that *T. massyae* is the juvenile of "*T. dussumieri*" Pfeffer, 1900, but we believe this is not so, especially if "*T. dussumieri*" Pfeffer and *P. boschmai* Adam are conspecific. The specimen of "*T. dussumieri*" Pfeffer, 1900 had a mantle length (ML) of 162 mm (sex and stage of maturity unknown). Clarke (1980) recorded nine specimens of *P. boschmai* from 240 to 580 mm ML, seven of which were mature or spent females. We have a male specimen of *T. massyae* of 105 ML (Museum of Victoria collections) that has developing testis, spermatophoric apparatus, and Needham's sac

(without spermatophores), so it must be approaching maturity and maximum size. At present too few specimens, of sufficient size range, of the two taxa of *Tetronychoteuthis* have been examined to enable us to be certain, but we believe that they are distinct species.

The ultimate solution of these problems lies in an examination of all extant type material, of voucher specimens, and of additional specimens. In the meantime, this summary should provide a basis from which future work can proceed.

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102(3), 1989, pp. 808–811

RHYSSOPLAX BALIENSIS, A NEW SPECIES OF CHITON FROM INDONESIA (MOLLUSCA: POLYPLACOPHORA: CHITONIDAE)

Robert C. Bullock

Abstract.—*Rhyssoplax baliensis* is described from Bali, Indonesia. It differs from *R. burmana* (Pilsbry, 1893) by its smooth jugum, central mucro on valve VIII, and slightly convex valve I; from *R. densilirata* (Pilsbry, 1893) by having a banded girdle and by its narrower longitudinal ribs which bend medially and are more nodulose and widely spaced; and from *R. vauclusensis* (Hedley & Hull, 1909) by its smooth jugum, more numerous and smoother ribs on the lateral triangle, and smoother, less inflated girdle scales.

A single example of a large chiton from Bali, Indonesia, in the collection of the Australian Museum, Sydney, represents an undescribed species of *Rhyssoplax.* While the study of many chiton species is made easier by the examination of numerous examples, I do not hesitate to describe the present species due to the specimen's distinctiveness, size, and excellent condition which allows a detailed comparison with related *Rhyssoplax* species.

Abbreviations used in the text: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; DMNH, Delaware Museum of Natural History, Greenville; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; and ZMK, Universitetets Zoologiske Museum, Copenhagen.

Class Polyplacophora Gray, 1821
Family Chitonidae Rafinesque, 1815
Genus *Rhyssoplax* Thiele, 1893

Use of *Rhyssoplax* at the generic level is not accepted by all malacologists. Van Belle (1978, 1983) and Kaas & Van Belle (1980) treated the group as a subgenus of *Chiton* Linnaeus, 1758. Morphological features of the valves of both genera exhibit great plasticity and often are unreliable as taxonomic characters at the generic level. However, substantial radular differences exist between *Chiton,* which is primarily a New World group, and *Rhyssoplax,* which is represented abundantly in the Indo-Pacific region (Bullock 1988a, b).

Rhyssoplax baliensis, new species
Figs. 1–4, 8–11

Holotype.—Australian Museum, Sydney, C.60874, collected by T. Dranga.

Type locality.—Bali Island, Indonesia. Depth not recorded.

Description.—Animal moderately large, 47 mm in length, 24 mm in width. Valves subcarinate, angle about 115°. Valve I slightly convex; postmucronal slope of valve VIII concave anteriorly, convex posteriorly. Mucro somewhat blunt, central on valve VIII. Jugal region smooth; central areas with about 23 thin, longitudinal ribs which are more numerous and occasionally joined toward jugum. Lateral triangle raised, with seven or eight faintly nodular, radiating ribs; nodules more pronounced along posterior margin of lateral triangle. Terminal areas with numerous nodular, sometimes bifurcate radial ribs; anterior valve with about

43 ribs; posterior valve with about 33 ribs. Valve color very light cream orange; jugum pinkish with reddish brown speckles; seven small, dark brown splotches on longitudinal ribs along anterior edge of lateral triangle, additional splotches along posterior margin; longitudinal and radial ribs speckled with reddish brown. Girdle yellowish white with several splotches or bands of dull green or brown. Interior of valves white with fleck of dull reddish brown on each side of posterior slope of callus near mucro.

Tegmentum: Ventral layer of suprategmentum laterally with wedgelike, nearly transparent shelf. Subtegmentum not developed toward jugum, present laterally as thin layer of small canals (Fig. 8).

Esthete pores: Megalopores, each with surrounding micropores, scattered across central area; round to slightly ovate megalopores 1.6 to 2.6 times as large as round to ovate micropores (Fig. 9).

Articulamentum: Central depression of intermediate valves with numerous transverse slits in jugal tract. Primary slit-ray consisting of series of very small holes. Secondary slit-ray present laterally. Insertion teeth finely grooved, not deeply pectinate; pectination of intermediate and posterior valves proceeding anteriorly to lateral margins of apophyses. Slit formula 8/1/15.

Radula: [not available].

Girdle elements: Scales moderately large, roundly triangular, moderately inflated. Extensive ventrolateral reticular sculpture mostly hidden by overlapping scales. Central area with 15–16 thin, moderately pronounced ribs. Apical region with pustules which may be smaller and linearly arranged distally and at sides. Apical shelf barely evident (Figs. 10, 11). Ventral scales closely packed, rectangular, length 104–120 μm, width 23–28 μm. Marginal spicules oblong, bluntly pointed distally, rounded proximally, length 119–135 μm, width 35–43 μm.

Remarks.—Morphological features of the valves and girdle scales indicate that *Rhyssoplax baliensis* is related to *R. vauclusensis* (Hedley & Hull, 1909) from southern Queensland and New South Wales, Australia (Iredale & Hull 1926); *R. densilirata* (Pilsbry, 1893), which occurs from the Philippine Islands [Ang (1967) as *Ischnochiton* (*Lepidozona*) *luzonicus* (Sowerby, 1841); and specimens in DMNH and ZMK] south to the Admiralty Islands (BMNH; see Fig. 6); and *R. burmana* (Pilsbry, 1893) from Waltair, India (BMNH; see Fig. 5), east to Burma. *Rhyssoplax baliensis* is differentiated from the sympatric *R. densilirata* by: (1) the narrower longitudinal ribs of the central area which bend medially, not laterally; (2) the ribs of the central area and lateral triangle which are more nodulose and widely spaced; (3) the fewer radial ribs on the end valves (about 43 on valve I and about 33 on valve VIII compared with up to 69 on valve I and up to 57 on valve VIII of *R. densilirata*); and (4) the banded girdle. The

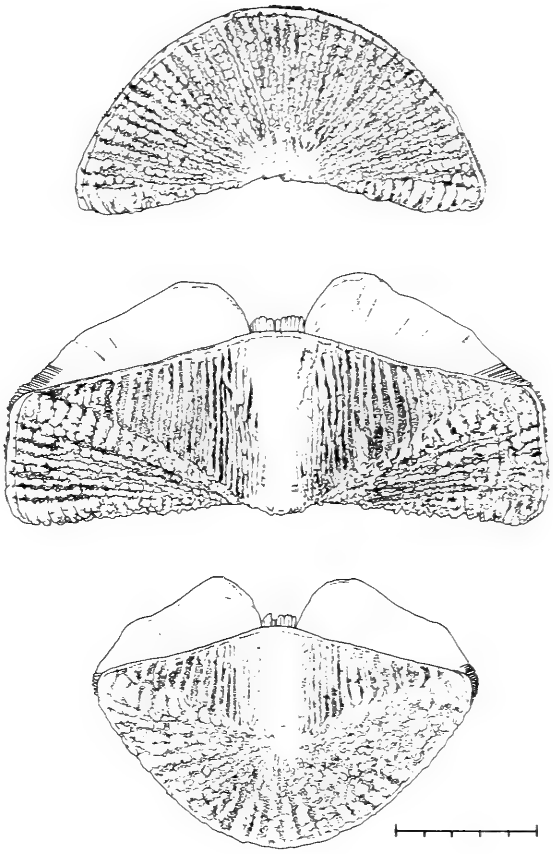
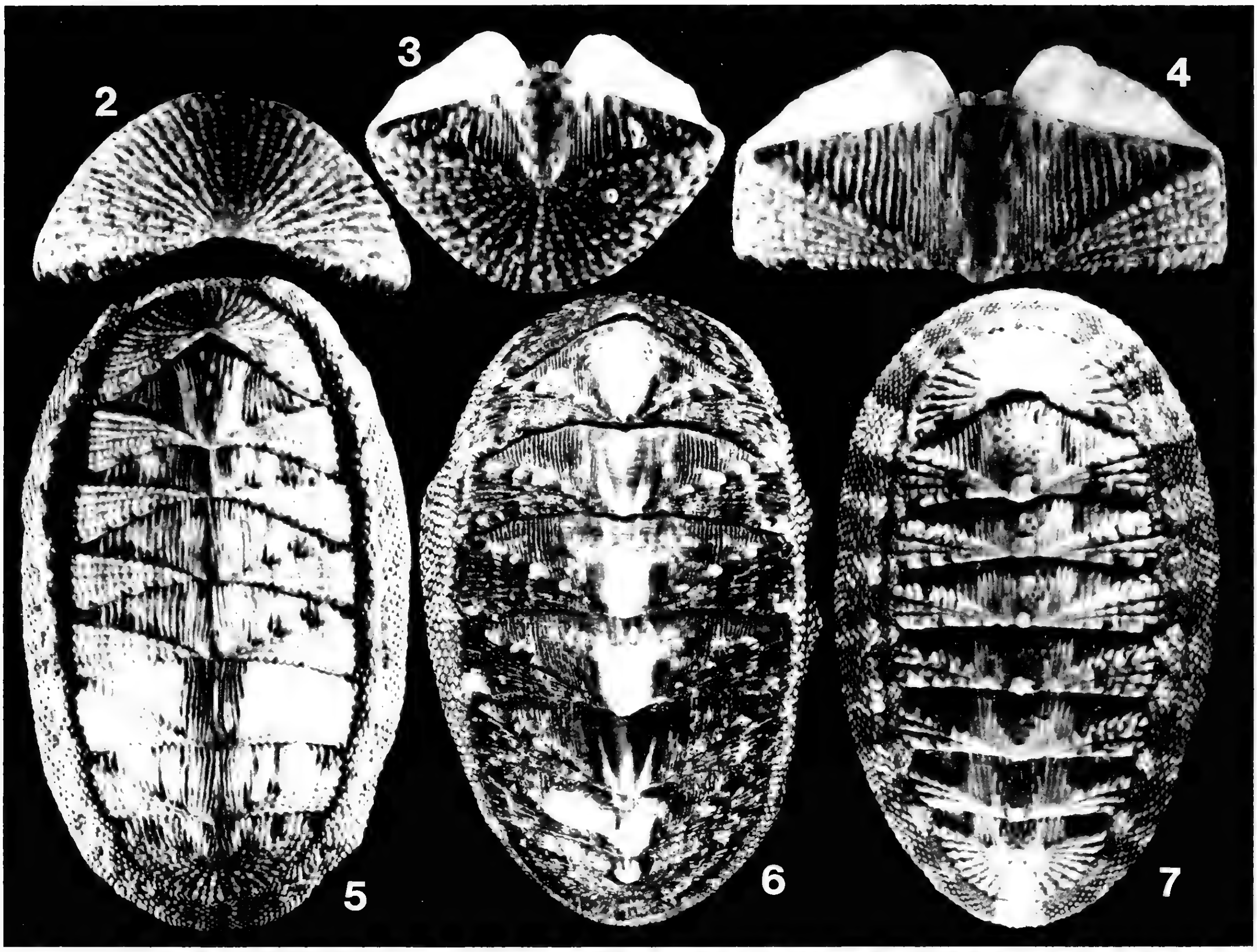


Fig. 1. *Rhyssoplax baliensis,* new species, holotype, AMS C.60874: Top, Anterior valve (I); Middle, Intermediate valve (IV); Lower, Posterior valve (VIII). Scale bar = 0.5 cm.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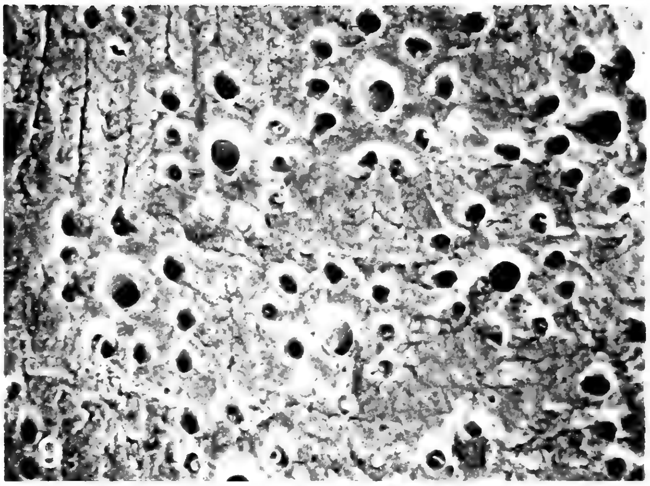
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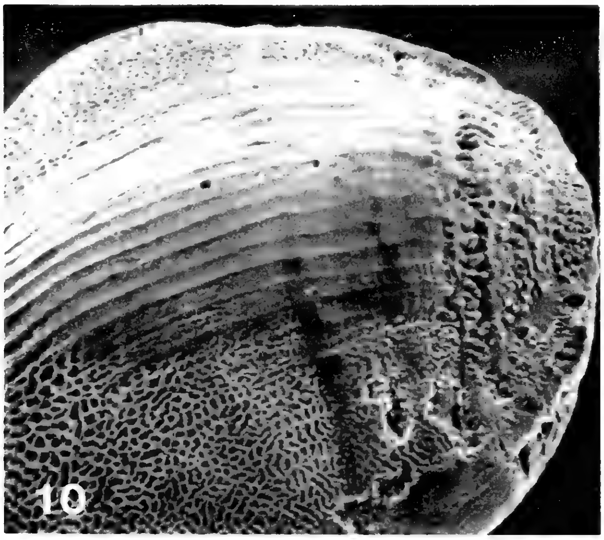
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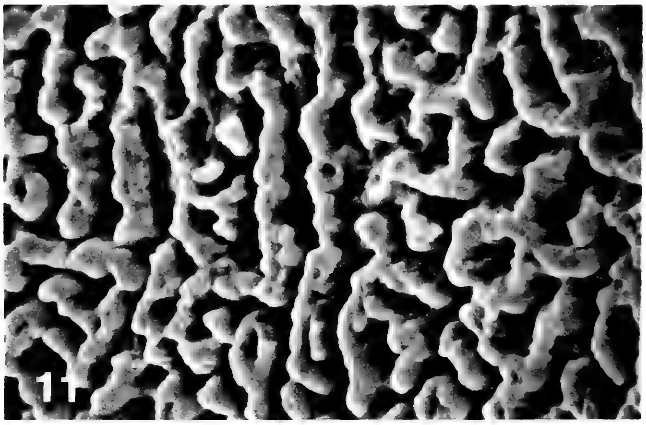
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girdle of examples of *R. densilirata* examined was never banded.

Rhyssoplax vauclusensis (Fig. 7) appears to be the closest known relative of *R. baliensis.* The former differs by having longitudinal ribs on the jugum, fewer, smoother radial ribs on the lateral triangle, and smoother, less inflated girdle scales with a cluster of elongate nodules distally on the apex.

Rhyssoplax burmana, which has conspicuous, narrow ribs on the central areas, differs from *R. baliensis* by its smaller size, ribbed jugum, slightly posteriorly acentric mucro on the posterior valve, fewer (4–6) ribs on the lateral triangle, and prominently concave anterior valve and postmucronal slope of the posterior valve.

Chiton vangoethemi Leloup, 1981, a recently described species from Madang Province, Papua New Guinea, differs from *R. baliensis* in its coloration, smooth jugal and central areas, and evenly rounded posterior outline of valve VIII. The smooth insertion teeth described by Leloup indicate that this species belongs in the Ischnochitonidae, not the Chitonidae.

Acknowledgments

I am grateful to W. Ponder (AMS), for the opportunity to study the sample of *Rhyssoplax baliensis.* I thank R. T. Abbott and R. Jensen (formerly DMNH), K. Boss (MCZ), G. Davis and R. Robertson (ANSP), and J. Taylor, J. Peake, and K. Way (BMNH) for the loan of comparative material. The scanning electron microscopy was done in the Department of Zoology and at the Graduate School of Oceanography, University of Rhode Island. The drawings of valves were provided by D. DeCarlo.

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Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881.

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Figs. 2–7. *Rhyssoplax baliensis* new species, *R. densilirata* (Pilsbry), *R. burmana* (Pilsbry), and *R. vauclusensis* (Hedley & Hull): 2–4, Anterior, intermediate, and posterior valves, respectively, of *R. baliensis,* holotype, AMS C.60874, width valve IV, 17.5 mm; 5, *R. densilirata,* Damma Is., Admiralty Is., BMNH 1899.4.12.3, 45 mm (slightly curled); 6, *R. burmana,* Waltair, India, BMNH 1952.11.19.62, 23 mm; 7, *R. vauclusensis,* Shellharbour, New South Wales, Australia, MCZ 204376, 27 mm.

Figs. 8–11. Scanning electron micrographs of valve and girdle scale morphology of *Rhyssoplax baliensis* new species: 8, Anterior tegmental innervation, ×70; 9, Esthete pores of central area, ×280; 10, Dorsal surface of girdle scale, ×137; 11, Ventrolateral reticular sculpture of girdle scale, ×665.

ANNOUNCEMENT

Copies of a "List of parasitic Copepoda in the collection of the Atlantic Reference Centre, St. Andrews, New Brunswick, Canada," are now available for distribution to interested individuals and institutions. The collection comprises lots representing 62 species of parasitic copepods from 13 families, ranging from commonly encountered to extremely rare and paratype specimens. The list includes data on hosts, localities, site of infection and number of specimens of each species. Copies are available by contacting:

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Systematics Laboratory
Huntsman Marine Science Centre
St. Andrews, New Brunswick, E0G 2X0
CANADA

APPLICATIONS PUBLISHED IN THE BULLETIN OF ZOOLOGICAL NOMENCLATURE

The following applications were published on 29 March 1989 in Vol. 46, Part 1 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

Case	
2668	*Drepanites* Mojsisovics, 1893 and *Hyphoplites* Spath, 1922 (Mollusca, Cephalopoda): proposed conservation.
2452	*Aphrodita imbricata* Linnaeus, 1767 (currently *Harmothoe imbricata*) and *Aphrodita minuta* Fabricius, 1780 (currently *Pholoe minuta*) (Annelida, Polychaeta): proposed conservation of the specific names.
2603	GRYLLACRIDOIDEA Stål, 1874 (Insecta, Orthoptera): proposed precedence over STENOPELMATOIDEA Burmeister, 1838.
2646	*Ptochus* Schönherr, 1826 (Insecta, Coleoptera): proposed conservation by confirmation of Marshall's (1916) designation of *Ptochus porcellus* Boheman in Schönherr, 1834 as the type species.
2680	*Euribia jaceana* Hering, 1935 (currently *Urophora jaceana*; Insecta, Diptera): proposed precedence over *Euribia conyzae* Hering, 1933.
2674	*Monograptus exiguus* (Graptolithina): proposed conservation of accepted usage by the citation of Lapworth (1876) as author.
2681	*Heliastes ovalis* F. Steindachner, 1900 (currently *Chromis ovalis*; Osteichthyes, Perciformes): proposed conservation of the specific name.
2527	*Heteronota pelagica* Girard, 1857 (currently *Gymnodactylus, Crytodactylus* or *Nactus pelagicus*; Reptilia, Sauria): proposed conservation of the specific name.

OPINIONS PUBLISHED IN THE BULLETIN OF ZOOLOGICAL NOMENCLATURE

The following Opinions were published on 29 March 1989 in Vol. 46, Part 3 of the *Bulletin of Zoological Nomenclature.*

Opinion No.

1518 *Harpa articularis* Lamarck, 1822 (Mollusca, Gastropoda): specific name conserved.

1519 *Ammonites neubergicus* Hauer, 1858 (Cephalopoda, Ammonoidea): to be given precedence over *Ammonites chrishna* Forbes, 1846.

1520 *Chagrinichnites brooksi* Feldmann, Osgood, Szmuc & Meinke, 1978 and *Chagrinichnites osboodi* Hannibal & Feldmann, 1983 (Trace fossil; arthropod): conserved.

1521 *Eriophyes* von Siebold, 1851 and *Phytoptus* Dujardin, 1851 (Arachnida, Acarina): *Phytoptus pyri* Pagenstecher, 1857 and *Phytoptus avellanae* Nalepa, 1889 designated as the respective type species.

1522 *Callianidea* H. Milne Edwards, 1837 (Crustacea, Decapoda): conserved.

1523 *Corisa germari* Fieber, 1848 (currently *Arctocorisa germari*; Insecta, Hemiptera): neotype designated.

1524 *Corisa distincta* Fieber, 1848 (currently *Sigara* (*Subsigara*) *distincta*; Insecta, Hemiptera): specific name conserved.

1525 *Phymatodes* Mulsant, 1839 and *Phymatestes* Pascoe, 1867 (Insecta, Coleoptera): conserved.

1526 *Nanophyes* Schoenherr, 1838 (Insecta, Coleoptera): conserved.

1527 *Polyommatus emolus* Godart, [1824] (currently *Anthene emolus*; Insecta, Lepidoptera): specific name conserved.

1528 *Pyralis nigricana* Fabricius, 1794 (currently in *Cydia* or *Laspeyresia*; Insecta, Lepidoptera): specific name conserved.

1529 *Ceutorhynchus* Germar, 1824, *Rhinoncus* Schoenherr, 1825 and *Curculio assimilis* Paykull, 1792 (Insecta, Diptera): conserved, and *Curculio assimilis* Paykull, 1792 and *Curculio pericarpius* Linnaeus, 1758 designated as the type species of *Ceutorhynchus* and *Rhinoncus* respectively.

1530 *Coeloides* Wesmael, 1838 (Insecta, Hymenoptera): *Coeloides scolyticida* Wesmael, 1838 designated as the type species.

1531 *Disophrys* Foerster, 1862 (Insecta, Hymenoptera): *Agathis caesa* Klug, 1835 designated as the type species.

1532 *Siphonosoma vastum* Selenka, De Man & Bülow, 1884, *Phascolosoma stephensoni* Stephen, 1942, *Phascolosoma scolops* Selenka, De Man & Bülow, 1884 and *Phascolosoma pacificum* Keferstein, 1866 (Sipuncula): specific names conserved.

1533 *Holothuria arenicola* Semper, 1868 (Echinodermata, Holothuroidea): specific name conserved.

1534 *Sternotherus* Gray, 1825 and *Pelusios* Wagler, 1830 (Reptilia, Testudines): conserved.

1535 *Halianassa studeri* von Meyer, 1838 (Mammalia, Sirenia): neotype designated; and *Halitherium* Kaup, 1838 (Mammalia, Sirenia): *Pugmeodon schinzii* Kaup, 1838 designated as the type species.

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Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

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102(4), 1989, pp. 815–825

MARIANACTIS BYTHIOS, A NEW GENUS AND SPECIES OF ACTINOSTOLID SEA ANEMONE (COELENTERATA: ACTINIARIA) FROM THE MARIANA VENTS

Daphne G. Fautin and Robert R. Hessler

Abstract.—We describe a new genus and species of sea anemone from the vicinity of hydrothermal vents in the Mariana back-arc basin, western North Pacific. Belonging to family Actinostolidae, *Marianactis bythios* is one of the most conspicuous animals around low temperature vents, at a depth of about 3600 m. Its mesenteries are not arrayed according to the *Actinostola* rule, it lacks basal tentacular thickenings, it has six pairs of complete mesenteries, and all its stronger mesenteries (members of the first three cycles) are gametogenic. It is further distinguished by having microbasic amastigophores in its tentacles. The final portion of Carlgren's (1949) key to the Actinostolidae is revised to accommodate *Marianactis* and other recent taxonomic changes in the family.

In April and May 1987, scientists discovered deep-sea hydrothermal vents and an associated faunal community in the Mariana back-arc basin, NNW of Guam, at a depth of about 3600 m. Far from the previously studied East Pacific Rise, these vents are unconnected to it by any intermediate spreading center.

Not surprisingly, much of the Mariana vent fauna is new (Hessler et al. 1988), including the relatively large sea anemone we describe here. One of the most conspicuous animals around low temperature vents, this member of family Actinostolidae belongs to a new genus and species, *Marianactis bythios* (Fig. 1). Actinians found on the Galapagos Spreading Center (Hessler & Smithey 1983) were too poorly preserved for detailed taxonomic study. The first species of actinian described from deep sea vents, *Cyananthea hydrothermala* Doumenc & Van-Praët, 1988, was collected on the French *Biocyatherm* 1 expedition around vents at 11°N in the Pacific, at 2000 m depth.

We detected no specializations to this unusual habitat in *M. bythios,* an anatomically unremarkable member of a predominantly deep water family. This ordinariness contrasts with many new species of other groups from vent habitats. *Marianactis* is distinguished by a suite of characters that individually occur in other of the approximately 20 genera comprising the Actinostolidae, as well as by microbasic amastigophores in its tentacles.

Materials and Methods

Field work relied on the submarine *Alvin.* Photographs were taken with a hand-held camera through the view ports, and with a Photosea M2000 stereocamera held by one of the mechanical arms. Video recordings were made with an Osprey video camera mounted on the same arm.

Eight specimens were collected using *Alvin*'s mechanical arm. Placed in an insulated container for transport to the surface, they were not exposed to temperatures higher than 10°C. Once on the surface, seven specimens were preserved in either 10% formalin or alcohol; one was initially frozen, and later formalin-preserved.

Paraffin sections 8 μm thick were stained with hematoxylin and eosin. Cnidae measurements were on undischarged capsules in squash preparations. In the section "Distribution and size of cnidae," "n" refers to the number of capsules measured, and "N" is the proportion of animals examined in which that type of cnida was present. A measurement in parentheses was from a single capsule falling considerably outside the range of the others. Not all tissues of each specimen were studied. Microscopy, including photomicrography, was with a Reichert Ultrastar equipped with Nomarski interference contrast optics, and an automatic exposure camera.

Marianactis, new genus

Definition.—Actinostolidae with well developed pedal disc. Column smooth; diameter about equal to height; mesoglea firm. Sphincter moderately strong; tentacles can be completely covered in retraction. Tentacles of uniform thickness entire length; outer much shorter than inner; arrayed in several cycles on marginal half of oral disc. Longitudinal tentacle and oral disc circular musculature ectodermal; that of tentacles equally well developed on all sides. Microbasic amastigophores in tentacles. Fewer tentacles than mesenteries. Mesenteries not arrayed according to *Actinostola* rule; six pairs complete; all stronger ones fertile; two symmetrically arrayed siphonoglyphs attach to directive mesenteries; retractor muscles diffuse, parietobasilar muscles present. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic amastigophores.

Type species.—*Marianactis bythios,* new species.

Etymology and gender.—The name *Marianactis* is a composite of "Mariana," geographical locality of the first known occurrence of this taxon, and "actis," Greek literally for ray or beam, a term that is applied to many taxa of sea anemones. The gender of "actis," and hence of *Marianctis,* is feminine.

Differential diagnosis.—Most members of Actinostolidae inhabit deep water and are therefore known primarily from preserved specimens. The genus *Marianactis* resembles many other genera of this family in being colorless (in preservation), in having relatively thick mesoglea, and in possessing tentacles that are wrinkled in preservation. It has the following combination of diagnostic characters: 1) mesenteries not arrayed according to the *Actinostola* rule, 2) no basal tentacular thickenings, 3) six pairs of complete mesenteries, and 4) all the stronger mesenteries (that is, members of the first three cycles) gametogenic. *Marianactis* is distinguished from all other actinostolids by its tentacular microbasic amastigophores.

Marianactis most resembles *Anthosactis* Danielssen, 1890, which has microbasic *b*-mastigophores in its stinging batteries, and unequally developed longitudinal tentacle musculature. It is also quite similar to *Tealidium* Hertwig, 1882, which is papillose. The definition of genus *Isoparactis* greatly resembles that of *Marianactis.* Carlgren (1949) included it among the Actinostolidae, using the definition of Stephenson (1920), who created it for *Paractis ferax* Stuckey, 1909. Parry (1952) demonstrated that Stuckey's species is actually an acontiate anemone belonging to family Bathyphelliidae.

All taxa were diagnosed initially with Carlgren (1949) and subsequently from the original literature. In Carlgren's (1949:77–78) key to the Actinostolidae, *Marianactis* falls under option II ("mesenteries not arrayed according to the *Actinostola*-rule"), B ("all or all stronger mesenteries fertile"). Beyond that, the key requires revision not only to accommodate *Marianactis.* Carlgren's descriptions of two additional genera of actinostolids were published posthumously—*Hadalanthus* Carlgren, 1956, and *Cnidanthea* Carlgren, 1959. In addition to *Isoparactis, Actinoscyphia* must be eliminated, because Riemann-Zürneck (1978) restored it to its own family. Also, Carlgren (1949) used the letter "h" in two separate couplets/triplets. The last two-thirds of the key is revised to read as follows:

- B) All or all stronger mesenteries fertile (with the possible exception of directives)
  - f) Longitudinal tentacle muscles mesogleal; at least 12 pairs of mesenteries complete
    - g) Outer tentacles with basal battery of microbasic *b*-mastigophores on aboral side. Submarginal collar. Directives may be sterile .... *Hormosoma*
    - gg) Microbasic *b*-mastigophores of tentacles scattered, not arrayed in batteries. Directives fertile .... *Cnidanthus*
  - ff) Longitudinal tentacle muscles ectodermal
    - h) Microbasic *b*-mastigophores in tentacles; arrayed in batteries and may also be scattered
      - i) Column with mesogleal papillae .... *Tealidium*
      - ii) Column smooth; longitudinal tentacle muscles strongest on oral side .... *Anthosactis*
    - hh) No microbasic *b*-mastigophores in tentacles
      - j) Microbasic amastigophores in tentacles; six pairs of mesenteries complete .... *Marianactis*
      - jj) Microbasic *p*-mastigophores in tentacles; six pairs of mesenteries complete; column divided into scapus and scapulus .... *Hadalanthus*
      - jjj) No tentacular mastigophores
        - k) At least 12 pairs of mesenteries perfect .... *Paranthus*
        - kk) Six pairs of mesenteries perfect
          - l) Sphincter very strong, forming a projecting wall. Mesenteries not hexamerously arrayed. Few, stout tentacles. May have distal papillae .... *Bathydactylus*
          - ll) Sphincter strong but not forming a wall. Mesenteries hexamerously arrayed. Column with papillose nematocyst batteries .... *Cnidanthea*
          - lll) Column smooth. More than 48 tentacles, closely packed at the rim, in at least 2 cycles .... *Epiparactis*
- BB) The oldest six pairs of mesenteries sterile, the other stronger mesenteries fertile
  - m) Column divisible into scapus and capitulum. Possibly two sphincters *Pseudoparactis*
  - mm) Column not divisible into scapus and capitulum .... *Antiparactis*
- BBB) The oldest 12 pairs of mesenteries sterile .... *Pycnanthus*
- BBBB) The three oldest cycles of mesenteries sterile. Mesenteries not divided into filament-free fertile and filament-bearing sterile ones. Oral disc lobed. Sphincter very long .... *Antholoba*

Fig. 1. Bed of *Marianactis bythios* in situ. Probe diameter 1 cm.

Marianactis bythios, new species

Description.—Body form and size: Expanded preserved specimens columnar and colorless (white to yellowish); column diameter approximately equal to height. Contracted preserved specimens dome-shaped; height one-half to two-thirds diameter. Field notes, and measurements on photos and video recordings, indicate that expanded animals (Fig. 1) were up to "five inches [i.e., about 130 mm] across" the tentacle crown, but preserved ones 15–50 mm diameter. Column appears rugose in some specimens, probably due to contraction; ectoderm thin relative to body wall (Figs. 2, 4, 5); often entirely sloughed off.

Base: Flat; equal to column width or somewhat larger; 15–50 mm. Adherent in life.

Tentacles and oral disc: Tentacles colorless in preservation, but photos and field observations note crowns pastel colored—mainly pinks and yellows. Tentacles arrayed in several cycles on peripheral half of oral disc; arise from indistinct margin where microbasic amastigophores may be densely packed (Fig. 6). Outer tentacles much shorter than inner; some outer tentacles merely stubs, inner to 15 mm length in animal 50 mm basal diameter. Tentacles taper slightly from base 1–2 mm in diameter to blunt point, but some swollen mid-way along length; transversely ridged in contraction; of equal thickness on all sides; lack basal thickenings. Fewer tentacles than mesenteries, but more than number of mesentery pairs; commonly about 60 tentacles. Oral disc capable of covering tentacles completely. Other details obscure due to contraction of most individuals examined.

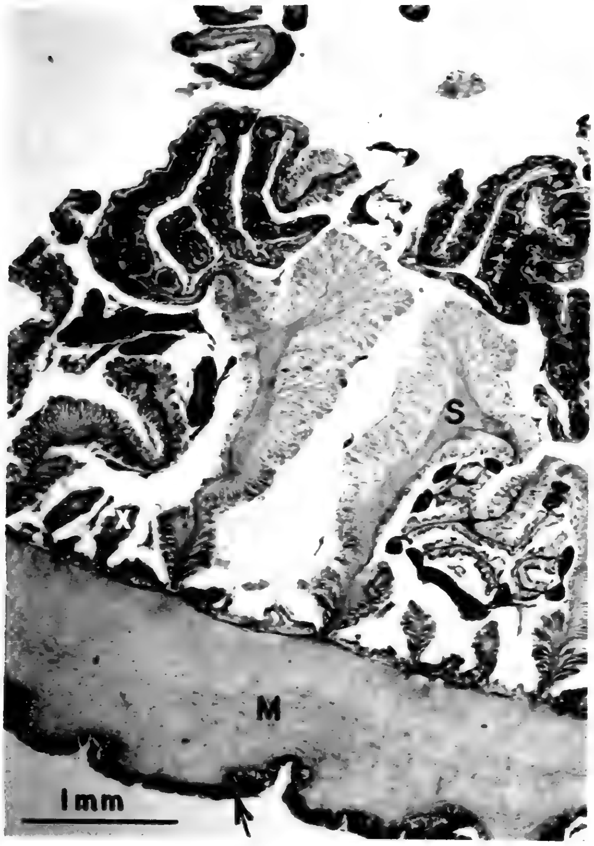

Fig. 2. Cross section of *Marianactis bythios* at mid-column. Note regular array of mesenteries and diffuse retractor muscles. Fourth cycle mesenteries (X) are minimally developed, secondary mesenteries (S) are fertile, column mesoglea (M) is thick, and ectoderm (arrow) is thin. CAS 065172 (holotype).

Fig. 3. Cross section through pair of fertile directive mesenteries, *Marianactis bythios*. CAS 065170.

Internal anatomy: Mesenteries regularly arrayed, not according to *Actinostola* rule (Fig. 2). Four cycles in most specimens; only first order complete and with small oral and marginal stomata; highest (fourth) order barely developed but seemingly wider proximally than distally, sterile, lacking filaments; filaments of penultimate (third) order absent from distal half. All except highest order (with possible exception of penultimate order in some individuals) fertile, including directives (Fig. 3). Only males seen; sexes presumably separate. Retractor muscles strong, diffuse, with increasingly wider processes centrally (Figs. 2, 3). Parietobasilar muscles with short detached pennon (Fig. 2); not evident at mid-body.

Sphincter muscle mesogleal, reticulate; composed of very small alveoli of uniform (Fig. 4) or slightly irregular (Fig. 5) size. Best developed at margin, tapering proximally; hugs endodermal side. Mesoglea on ectodermal side fibrous (Fig. 4).

Longitudinal musculature of tentacles strong, ectodermal; circular muscles not apparent. Oral disc circular muscles ectodermal, disrupted where tentacles insert on oral disc (Fig. 7).

Actinopharynx of typical actinostolid length and rugosity; white in color or rarely violet-brown (as is common in deep-water actinians); two symmetrical siphonoglyphs attach to directive mesenteries; siphonoglyphs not especially prolonged.

Cnidom: basitrichs, microbasic *p*-mastigophores, spirocysts, microbasic amastigophores.

Fig. 4. Longitudinal section of mesogleal sphincter of *Marianactis bythios.* CAS 065171.

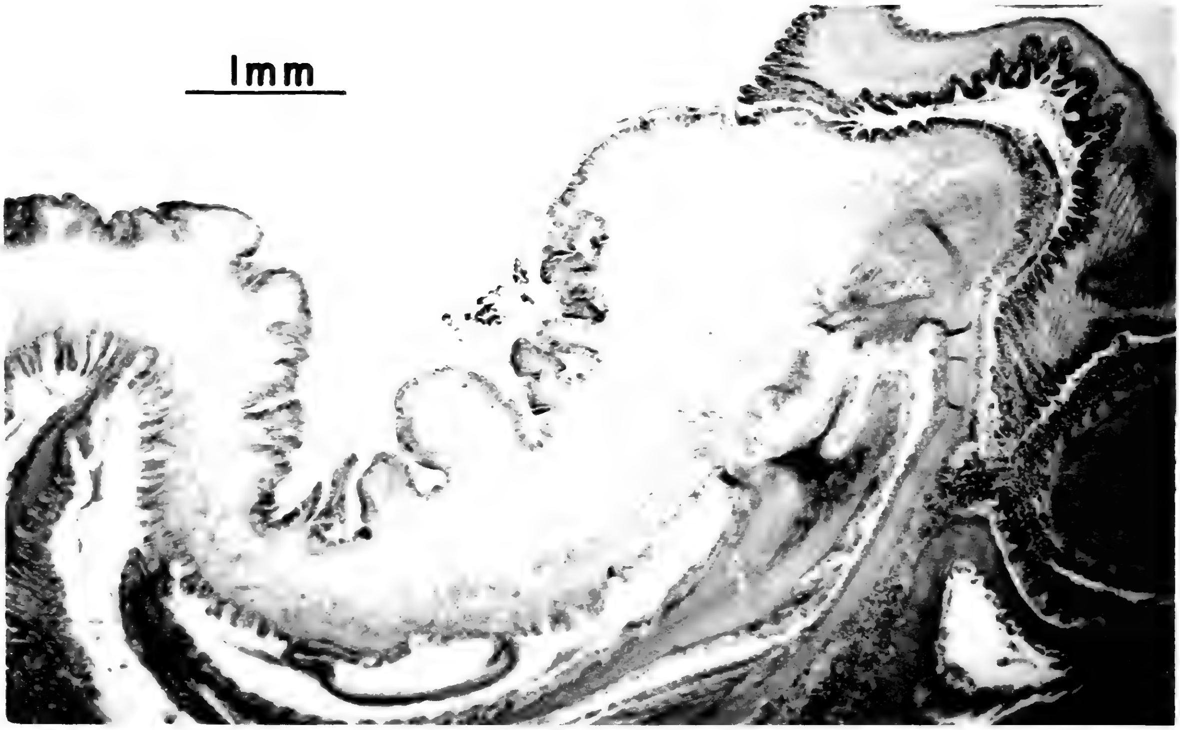

Fig. 5. Longitudinal section of mesogleal sphincter of *Marianactis bythios.* CAS 065172.

Fig. 6. Intersection of column and tentacles. Arrow indicates layer of microbasic amastigophores, *Marianactis bythios.* CAS 065172.

Distribution and size of cnidae.—(Letter corresponds to illustration in Fig. 8.)

Tentacles:
- spirocysts (A) (26.1) 27.5–49.2 (54.9) × 2.5–4.7 μm n = 41 N = 4/4
- robust spirocysts (B) 43.6–73.1 × 4.6–7.9 μm n = 35 N = 4/4
- basitrichs (C) 35.3–42.3 × 2.5–4.9 μm n = 34 N = 4/4
- microbasic amastigophores (D) 29.8–36.0 × 4.3–5.0 (5.4) μm n = 18 N = 2/3

Actinopharynx:
- microbasic *p*-mastigophores (E) (27.3) 30.4–45.9 × 4.3–6.0 μm n = 36 N = 3/3

Mesenterial filaments:
- microbasic *p*-mastigophores (F) 28.4–44.3 (48.0) × (3.9) 4.2–6.2 μm n = 44 N = 4/4

Column:
- basitrichs (G) (19.1) 20.3–27.3 (27.8) × 2.3–3.7 μm n = 44 N = 4/4

Discussion.—Habitat, range, and natural history: The eight specimens of *Marianactis bythios* examined were collected from the Anemone Heaven portion of the Burke hydrothermal field (18°10.9′N, 144°43.2′E, 3660 m) and from the Alice Springs site (18°12.6′N, 144°42.4′E, average depth 3640 m). All were originally attached to rocks, although some were detached during collection.

Members of this species were the dominant inhabitants of the region peripheral to the vent openings. Population density was high in places, but tentacles of adjacent individuals generally did not make contact; the animals seemed to be evenly spaced. At both sites, the plume of vent water appeared quite "smoky." Where emerging vent water was clear, such as at the Ilium field and the Snail Pits portion of the Burke field, this anemone occurred in smaller numbers. We can offer no explanation for this correlation.

Even individuals attached to rock near

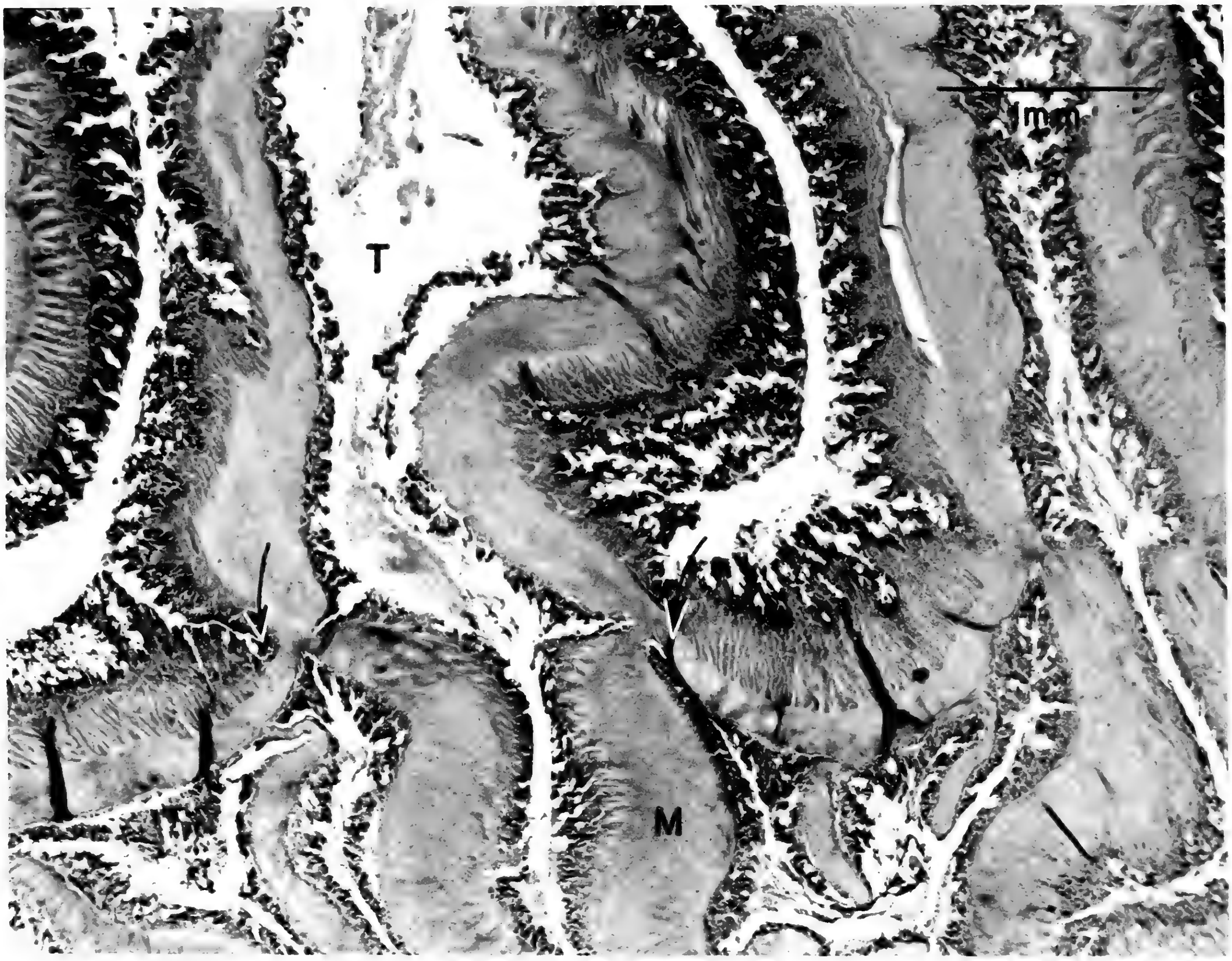

Fig. 7. Longitudinal section of *Marianactus bythios* at intersection of tentacles and oral disc. T = coelenteric space within tentacle; M = mesentery; arrows = region lacking ectodermal muscles. MNHN specimen.

the lip of the openings were never positioned where they were exposed to undiluted emerging vent water, unlike some crabs, snails, and shrimps, which occurred in the vent openings themselves. Therefore, it is unlikely that the actinians contacted water in excess of a degree or so over ambient, which is 1.6°C; more than a meter from the vent, water temperature was essentially ambient. At both sites, abundance of actinians declined with distance from the vent opening. They extended tens of meters from the emerging water, being found further from vent openings than organisms of any other taxa associated with the vents. The outermost edge of their distribution operationally defined the periphery of the vent field.

Many shallow water sea anemones possess intracellular algal symbionts that provide fixed carbon to their hosts (e.g., Muscatine 1974). Morphological and behavioral adaptations to them have evolved in some species (e.g., Lewis 1984). Several invertebrate taxa associated with hydrothermal vents bear endosymbiotic bacteria that oxidize reduced compounds (sulfide, methane), providing an energy source for their hosts (Childress et al. 1987; Stein et al. 1988). Therefore, we were especially alert for morphological evidence of symbionts in this anemone, but found none. Doumenc & Van-Praët (1988) concluded that the diet of the vent actinian *Cyananthea hydrothermala* includes bacteria, but that they are not in symbiosis.

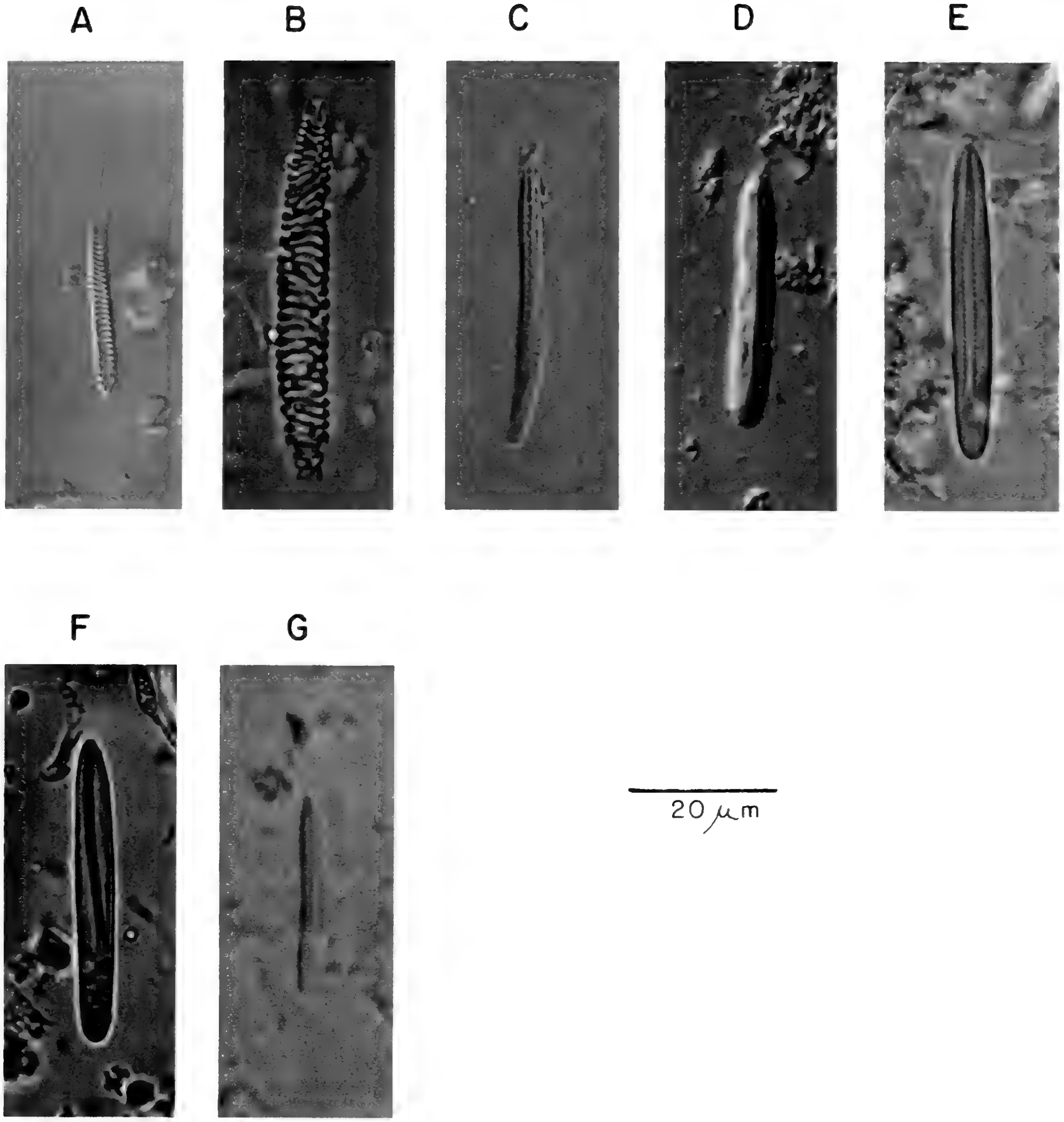

Fig. 8. Cnidae signature of *Marianactis bythios.* See text for explanation.

Nematocyst batteries: Whether the microbasic amastigophores of the tentacles are organized into batteries is uncertain. That type of cnida seems absent altogether from some individuals, and scattered in the tentacles of others. But the holotype has a dense layer of them (Fig. 6) in what is either the distalmost column or basalmost tentacles—with no distinct margin, a dividing line cannot be drawn. Carlgren's (1949) catalog refers repeatedly to nematocyst batteries, but contains no definition of the term. At least for actinostolids, the implication is that the microbasic *b*-mastigophores in stinging batteries are extraordinarily large (e.g., Carlgren 1921, in the description of *Tealidium jungerseni*). The microbasic amastigophores of *M. bythios* are of unremarkable size.

Comparison with other vent species: The description of *Cyananthea hydrothermala* Doumenc & Van-Praët, 1988, the only previously described vent actinian, is incomplete and tentative, being based on a portion of one poorly preserved specimen. Thus, some of its anatomy had to be inferred, and its attribution to family Actinostolidae was mainly due to the absence of acontia. Indeed, critical features such as mesenterial arrangement and whether nematocyst batteries are present seemingly could not be determined; hence our omission of it from our revised key. *Marianactis bythios* clearly differs from this species in cnidae (specifically tentacle basitrichs and spirocysts of our species are larger, and ours lacks columnar microbasic *p*-mastigophores), in tentacle arrangement, and in color.

Phylogenetic relationships within the Actinostolidae: Many genera of actinostolids, as is true in some other actinian families, are defined by unique combinations of characters rather than by singular features. It is this mosaic nature of diagnostic characters that makes inferences about evolution difficult.

Etymology: The specific epithet *bythios* means "of the deep" in Greek.

Type Locality and Specimens

Holotype.—Department of Invertebrate Zoology, California Academy of Sciences (CAS), catalog #065172; male; from Alice Springs, Mariana back-arc basin. Includes 10 microscope slides from it.

Paratypes.—CAS #065171; two specimens, one sectioned (male); from Anemone Heaven, Mariana back-arc basin. Includes 10 microscope slides from sectioned specimen.

CAS #065170; one specimen; male; from Alice Springs, Mariana back-arc basin. Includes 10 microscope slides from it.

National Museum of Natural History (USNM), catalog #84401; one specimen; from Burke field, Mariana back-arc basin; includes 10 microscope slides from it.

USNM #84402; one specimen; from Alice Springs, Mariana back-arc basin.

Museum Nationale d'Histoire Naturelle, Paris (MNHN); one specimen; from Burke field, Mariana back-arc basin.

MNHN; one specimen; from Alice Springs, Mariana back-arc basin; includes 10 microscope slides from it.

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A REVISION OF THE GENUS *ASPIDOSIPHON* (SIPUNCULA: ASPIDOSIPHONIDAE)

Edward B. Cutler and Norma J. Cutler

Abstract.—The 64 putative species of the sipunculan genus *Aspidosiphon* and the morphological characters used to differentiate them are critically reviewed. The monograph of Stephen & Edmonds (1972) is used as a starting place and all changes made in the intervening years are reiterated here. All available type material was studied and new collections of Hawaiian and Caribbean material are used to analyze within-deme variation. Hook and anal shield morphology are determined to be broadly useful at the species level, four characters (longitudinal muscle layer, retractor muscle origins, caudal shield, nephridia length) in a more restricted manner to separate subgroups, and three (introvert/trunk angle, bifurcated anterior spindle muscle, loosely wound gut coil) are useful in special cases. A new subgenus, *Aspidosiphon* (*Akrikos*), is proposed for those five species lacking hooks in rings. A key to, and a discussion of, the 19 remaining species (plus one reduced to subspecies) with the newly designated synonyms are presented. A brief statement of the distribution of each species is given. An overall summary of the zoogeography and habitat shows more endemic species are found in the warm water regions of the Atlantic Ocean than in the Indo-West Pacific, and that only 42% of *Aspidosiphon* species live in coral or rock.

This continues our revisionary series on the species of sipunculan worms (e.g., Cutler & Cutler 1985a, b, 1986, 1987b, 1988). With this work we complete our examination of all the genera in this phylum except *Phascolosoma,* which is in preparation. The monograph of Stephen & Edmonds (1972) is the starting place for this work (48 species names). Also included (Table 1) are the 11 species erected since that time, the two species transferred into this genus, and the three resurrected names.

The genus *Aspidosiphon* was erected by Diesing in 1851, and was placed in its own family, Aspidosiphonidae, by Baird (1868) in the order Aspidosiphoniformes Cutler & Gibbs (1985). The name *Paraspidosiphon* was proposed by Stephen in 1964 as a genus for those species with the longitudinal muscle layer separated into bundles. Cutler (1973) reduced it to subgeneric rank and this has been followed by most other authors (see discussion below).

Whenever possible we have obtained type material to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to evaluate better the traditionally used morphological characters. Recent collecting trips to Hawaii, Curacao and Venezuela (Cumana and Isla de Los Roques) have greatly facilitated this effort. The opportunity to observe living material is invaluable. Parts of these collections will be deposited in the National Museum of Natural History, Washington, D.C. as reference material.

We first discuss the morphological characters in light of our recent analyses, then discuss those taxa not clearly belonging to this genus. Following are a key to all the species we consider valid, a section where each of these species is discussed including a synonomy, a discussion of any newly added junior synonyms, and a summary of the known distribution of each species. A short zoogeographical summary of the genus concludes this work.

For clarity in the Morphological Characters section, the recent work of Saiz Salinas (1984) needs to be mentioned here. His redescription of Quatrefages' 1865 species from the Paris Museum has led to the elevation of *A. coyi* and *A. laevis* as senior synonyms of the more familiar *A. truncatus* for the former and the large *A. cumingii/klunzingeri* complex for the latter. In both cases holotypes are now available to science, which is not the case for the more familiar names. In some ways this action is analogous to that of Rice & Stephen (1970) where they resurrected the older and long unused names of Gray and Baird.

The following abbreviations are used in the text for the museums from which we borrowed material: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHU); Musée Océanographique Monaco (MOMV); Naturhistoriska Riksmuseet, Stockholm (NHRS); Royal Scottish Museum, Edinburgh (RSME); National Museum of Natural History, Washington (USNM); Zoologisk Museum, Copenhagen (UZMK); Zoological Institute, Academy of Science, Leningrad (ZIAS); Zoological Institute, Tohoku University, Sendai (ZITU); Zoölogisch Museum, Universiteit van Amsterdam (ZMUA); Zoological Museum, University Bergen (ZMUB); Zoologisches Museum, Universität Hamburg (ZMUH).

Morphological Characters

1. Introvert hooks and spines.—As in most genera, the introvert bears (in all but three species) some array of specialized structures usually referred to as hooks. Voss-Foucart et al. (1977) have shown these to lack chitin but consist of a horny protein. Many hooks are arranged in regular rings around the distal portion of the introvert and may have either one or two points (uni- or bidentate). On some species scattered hooks also are found proximally and in two species only scattered hooks are found. Additionally, epidermal structures of varying sizes and shapes called spines are arranged in a random manner on the proximal portion of the introvert. Examination of the literature reveals that the term "spine" meant different things to different authors, sometimes being used as a synonym for what others would term "unidentate hook." Since hooks and spines come in a wide variety of arrangements, sizes, and shapes, and often grade into one another, it is easy to understand the genesis of this problem that is unique to *Aspidosiphon*. We will attempt some clarification and definitions.

In the phylum Sipuncula, the term "hook" has been applied to structures having a wide variety of shapes, sizes, and arrangement. It is clear that a *Themiste* hook is different from a *Nephasoma* hook and that both differ from *Phascolosoma* hooks. Structures that have been called "spines" are similar to "hooks" of *Themiste* and of some *Phascolion* species. We now propose calling all of these introvert structures hooks. The term "spine" will be restricted to conical pointed anal shield units. The hook's apex points posteriorly (away from the mouth) with the convex curvature being anterior.

The different types of hooks are defined as follows:

> Type A: *Compressed hooks.*—Usually arranged in rings, occasionally scattered, laterally compressed, and having, in a side view, a distinct posterior curve. These may be unidentate or bidentate (Fig. 1A, B). When a secondary tooth is present it may be variable in size, sometimes reduced to a

Table 1.—Original and proposed names of the *Aspidosiphon* species.

Subgenus *Aspidosiphon* s.s.	
Aspidosiphon albus Murina, 1967	no change*
Aspidosiphon brocki Augener, 1903	*A. elegans*
Aspidosiphon carolinus Sato, 1935	*A. elegans*
Aspidosiphon cylindricus Horst, 1899	*species inquirenda*
Aspidosiphon elegans (Chamisso & Eysenhardt, 1821)	no change
Aspidosiphon exhaustus Sluiter, 1912	*A. muelleri*
Aspidosiphon exiguus Edmonds, 1974	no change
Aspidosiphon exilis Sluiter, 1886	*A. elegans*
Aspidosiphon gerouldi ten Broeke, 1925	*A. misakiensis*
Aspidosiphon gosnoldi Cutler, 1981	no change
Aspidosiphon gracilis (Baird, 1868)	no change
Aspidosiphon hartmeyeri Fischer, 1919	*A. misakiensis*
Aspidosiphon hispitrofus LiGreci, 1980	*A. muelleri*
Aspidosiphon homomyarius Johnson, 1964	*A. elegans*
Aspidosiphon imbellis Sluiter, 1902	*A. muelleri*
Aspidosiphon inquilinis Sluiter, 1902	*A. muelleri*
Aspidosiphon jukesii Baird, 1873	*A. muelleri*
Aspidosiphon kovaleskii Murina, 1964	*A. muelleri*
Aspidosiphon longirhyncus Cutler & Cutler, 1980	*A. mexicanus**
Aspidosiphon macer (Sluiter, 1891)	*species inquirenda*
Aspidosiphon mexicanus (Murina, 1967)	no change*
Aspidosiphon misakiensis Ikeda, 1904	no change
Aspidosiphon muelleri Diesing, 1851	no change
Aspidosiphon ravus Sluiter, 1886	*A. elegans*
Aspidosiphon spinalis Ikeda, 1904	*A. elegans*
Aspidosiphon spinosus Sluiter, 1902	*A. elegans*
Aspidosiphon spiralis Sluiter, 1902	no change
Aspidosiphon thomassini Cutler & Cutler, 1979	no change*
Aspidosiphon tortus Selenka, de Man & Bülow, 1883	*A. muelleri*
Aspidosiphon venabulum Selenka, de Man & Bülow, 1883	no change*
Aspidosiphon zinni Cutler, 1969	no change*
Subgenus *Paraspidosiphon*	
Aspidosiphon ambonensis Augener, 1903	*A. tenuis*
Aspidosiphon angulatus Ikeda, 1904	*A. laevis*
Aspidosiphon brasiliensis Cordero & Mello-Leitao, 1952	*A. laevis*
Aspidosiphon coyi Quatrefages, 1865	no change
Aspidosiphon cumingii Baird, 1868	*A. laevis*
Aspidosiphon exostomus Johnson, 1964	*A. steenstrupii*
Aspidosiphon fischeri ten Broeke, 1925	no change
Aspidosiphon formosanus Sato, 1939	*A. tenuis*
Aspidosiphon gigas Sluiter, 1884	*A. laevis*
Aspidosiphon grandis Sato, 1939	*A. laevis*
Aspidosiphon havelockensis Haldar, 1978	*A. tenuis*
Aspidosiphon insularis Lanchester, 1905	*Phascolosoma perlucens*
Aspidosiphon johnstoni Edmonds, 1980	*A. laevis*
Aspidosiphon klunzingeri Selenka, de Man & Bülow, 1883	*A. laevis*
Aspidosiphon laevis Quatrefages, 1865	no change
Aspidosiphon levis Sluiter, 1886	*A. tenuis*
Aspidosiphon major Vaillant, 1871	*A. laevis*
Aspidosiphon makoensis Sato, 1939	*A. steenstrupii*
Aspidosiphon ochrus Cutler & Cutler, 1979	*A. steenstrupii*
Aspidosiphon pachydermatus Wesenberg-Lund, 1937	*A. laevis*
Aspidosiphon parvulus Gerould, 1913	no change

Table 1.—Continued.

Aspidosiphon planoscutatus Murina, 1968	no change
Aspidosiphon quatrefagesi Saiz Salinas, 1984	*A. laevis*
Aspidosiphon pygmaeus Fischer, 1921	*A. muelleri*
Aspidosiphon schnehageni Fischer, 1913	*A. gracilis schnehageni*
Aspidosiphon semperi ten Broeke, 1925	*A. steenstrupii*
Aspidosiphon speciosus Gerould, 1913	*A. laevis*
Aspidosiphon speculator Selenka, 1885	*A. steenstrupii*
Aspidosiphon spinososcutatus Fischer, 1922	*A. parvulus*
Aspidosiphon steenstrupii Diesing, 1859	no change
Aspidosiphon tenuis Sluiter, 1886	no change
Aspidosiphon trinidensis Cordero & Mello-Leitao, 1952	*A. steenstrupii*
Aspidosiphon truncatus (Keferstein, 1867)	*A. coyi*
Golfingia mokyevskii Murina, 1964	*Antillesoma antillarum*

* Now in new subgenus *A.* (*Akrikos*).

small knob. A transition zone in some species exists at the proximal end of the rings of hooks where one may find a gradual widening of the anterior base of the unidentate hooks. Sometimes these scattered hooks are rounded at the anterior-lateral corners but still compressed posteriorly looking like a ship's stout mast and sail.

Type B: *Pyramidal hooks.*—Have triangular bases, the anterior side of which is shorter than the lateral sides, are usually less curved than Types A or C, are variably pigmented (dark to light), and translucent (Fig. 1E, F). The borderline between Types A and B is not clear in all species.

Type C: *Conical hooks.*—Have a nearly circular cross section (cone shape), a gentle posterior curve, and are usually opaque and dark colored (Fig. 1C, D). This type is found on the dorsal side of *A. elegans*' introverts.

When introvert skin is removed and placed on a slide in a drop of glycerin for closer examination, the orientation of these hooks can add to the confusion. If viewed from the anterior or posterior (instead of laterally), scattered unidentate compressed hooks look very much like pyramidal hooks (Fig. 1G). However, a compressed hook has a narrower base. Further distortion can be caused if the hooks are not lying flat on the slide. Scanning electron micrographs can help reveal the natural configurations and the three dimensionality of these structures.

The shape of the clear area (less dense to transmitted light) in the hook has limited taxonomic value. In most species there is an ill-defined triangular area, but in *A. steenstrupii* and *A. elegans* there is a thin, posteriorly directed, tongue-like extension (Fig. 2).

The height of the hook has sometimes been used as a diagnostic character, but this has limitations. The unidentate *A. laevis* complex (as defined below) shows a clear correlation between trunk size and hook size (5–10 mm worms have 20–40 μm hooks, 20–30 mm worms have 40–60 μm hooks, and 40–70 mm worms have 60–80 μm hooks). The same pattern is shown by an analysis of 32 specimens of *A. steenstrupii* ranging in trunk length from 7–50 mm. Hook size varied from 30–90 μm with larger worms having larger hooks (a linear regression of these data gave a positive slope of 0.89). Therefore, hook size should not be considered in isolation from trunk size. Despite this a clear pattern does appear with certain species (e.g., the members of the new subgenus proposed here) always having small hooks (under 30 μm) and some species

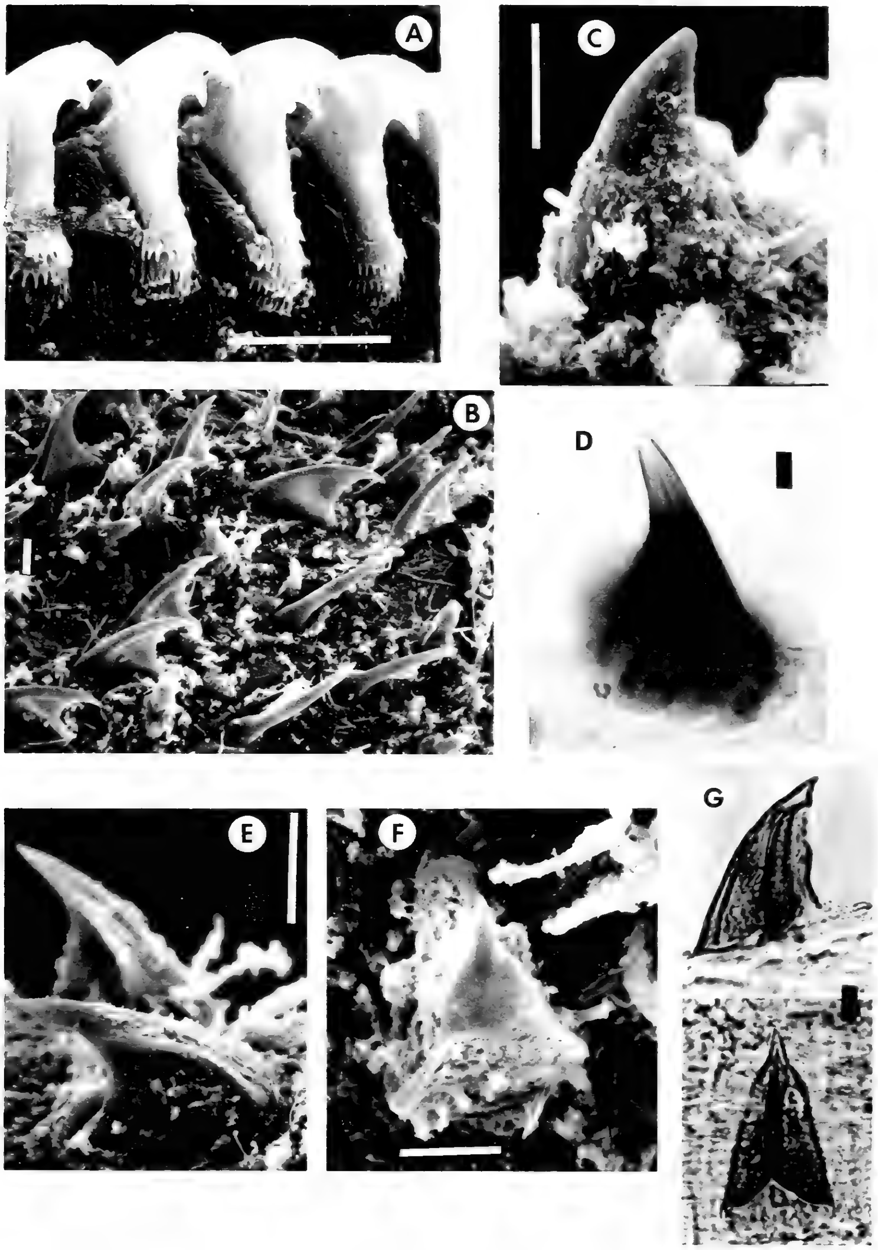

Fig. 1. Introvert hooks: A, Compressed, bidentate (Type A) from *A. muelleri,* posterior view; B, Compressed unidentate (Type A) from *A. misakiensis*; C–D, Conical (Type C) from *A. elegans*; E, Pyramidal (Type B) from *A. parvulus*; F, Pyramidal (Type B) from *A. steenstrupii* viewed from above; G, Pyramidal (Type B) from *A. steenstrupii,* different angles on light microscope. Scale line = 10 μm, for G = 20 μm.

with only larger hooks. The central problem is that many species have both large and small hooks.

In general, some species lack unidentate hooks, some lack bidentate hooks, some have both Type A and B hooks while others have only Type A hooks. Certain species will have both kinds of compressed and Type B hooks. In summary, if one examines the most distal rings of hooks and differentiates between unidentate Type A and Type B hooks, hook morphology can be useful to the systematist in almost all cases and hook size can help in some cases.

2. Anal shield (degree of development, nature of units, grooves).—At the anterior end of the trunk, horny protein (not chitin) forms an array of cuticular units varying in degree of development (Voss-Foucart et al. 1977). At one extreme is *A. mexicanus* or *A. thomassini* with a collection of small scattered units sometimes looking more like an area

Fig. 2. Internal hook structure: A, *A. elegans,* B, *A. steenstrupii,* C, *A. tenuis.* Note absence of tongue-like extension in C. Scale lines = 20 μm.

of rough skin. At the other end of the continuum is *A. laevis* or most *A. muelleri* where the units are compacted to form a thick, dark, solid mass. These two species are among those that have shields with well developed longitudinal and/or transverse grooves. When a shield has aggregations of units separated by grooves we refer to these aggregations as plates. The shield nearest the mid-dorsal anus is the dorsal part while that nearest the introvert is the ventral part.

The nature of the shield units may undergo slight changes with age (see *A. jukesii* in Cutler & Cutler 1979a:970) and may be modified by the size/shape of the shell (gastropod vs. scaphopod) or other space occupied by the worm. When the introvert is retracted this shield functions as an operculum. While some within-deme variation does exist, the morphology of the anal shield is consistent enough and distinct enough to be useful to the systematist.

3. Caudal shield (degree of development).—At the posterior end of the trunk there is a epidermal structure (horny protein) present in most (but not all) species. This shield assumes various forms in living worms and, therefore, when preserved, can also vary from rather flat to pointed to pagoda shaped. They have a variable number of radially arranged grooves or furrows, but this attribute is not species specific. Even within a deme the degree of development (thickness) varies (Fig. 3). In a species with extensive historical data indicating a "normal" shield, one may find individuals with very weakly developed shields. In such animals the shield may be reduced to some papillae and only a vague suggestion of a chitinoid layer. It is probable that in many species the genetic potential is there, but its expression is variable and responds to environmental stimuli or age. Some species (*A. laevis*) always have a shield and others (e.g., *A. mexicanus* or *A. zinni*) never do. When a shield is present, there is little to distinguish one species from another using this character. Therefore, aside from presence/absence, the caudal shield has limited value to the systematist.

4. Introvert retractor muscles (origin, degree of fusion).—The single pair of long muscles used to retract the introvert insert at the anterior end and originate from the ventral trunk wall in the posterior third of the worm. The placement of these origins (attachment) is usually included in species descriptions, often with a significant lack of precision (near the posterior end, in the last quarter), but sometimes it is used as a diagnostic (or key) character. While in other genera we have found that retractor origins appear to shift anteriad as the animal grows (zone of trunk growth being posterior to the origins), it is difficult to generalize about this in *Aspidosiphon.* If one calculates the dis-

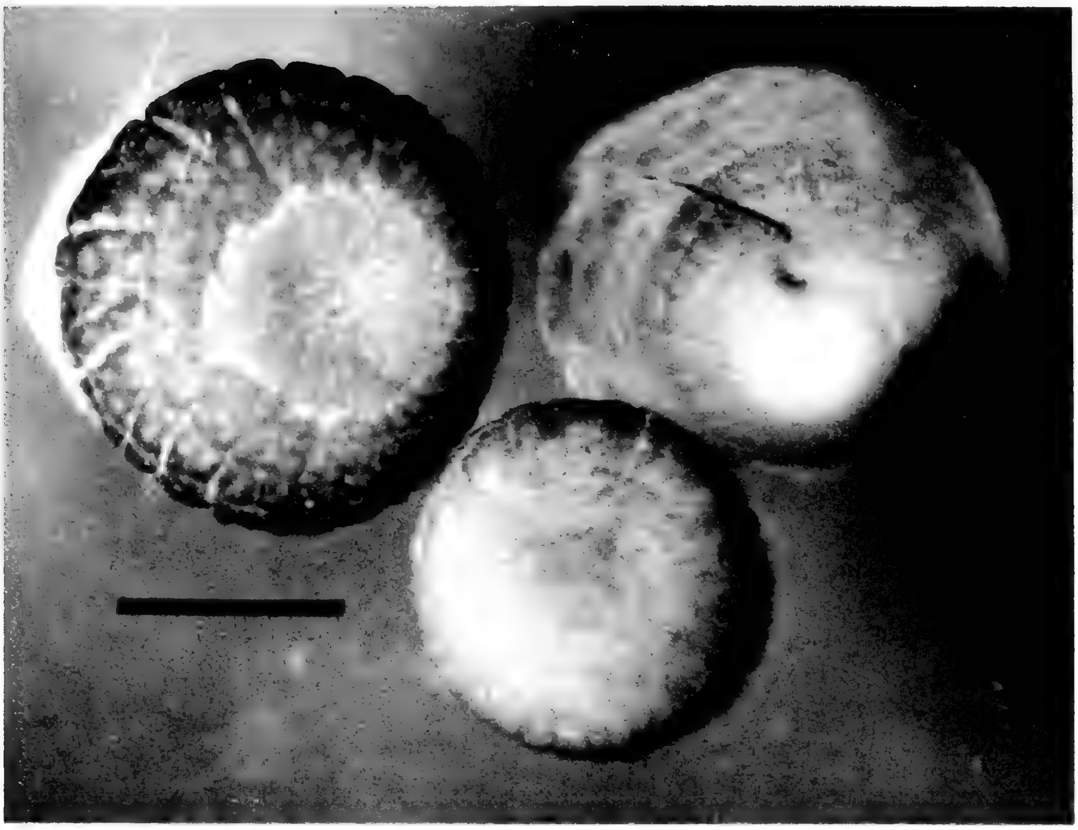

Fig. 3. Caudal shields of *A. elegans.* Three 17 mm worms from one deme in Ponape to show variation in degree of development. Scale line = 1 mm.

tance as a percentage of trunk length, there do seem to be some species where this value remains reasonably constant over a wide range of sizes (e.g., *A. muelleri,* 95–100%). However, other species exhibit more variation (see Table 2 for *A. elegans,* 65–85% and *A. steenstrupii,* 70–90%). This is not clearly correlated with size. Therefore, while this attribute can be useful for differentiating two subsets, it does not have value at the species level.

The second aspect of this complex that is sometimes noted is the degree of fusion between these two muscles. In the older literature there is considerable confusion on this matter, such that some descriptions allege there to be only one or as many as four, or one muscle with one, two or four "roots." From what we know about the ontogeny of this functional complex in sipunculans, it is probable that they all begin life with two pairs of retractors (Rice 1976). The dorsal pair is lost and the ventral pair fuses to varying degrees. However, quantifying this is extremely difficult because extension of the introvert will stretch out the muscle and the point of fusion will move away from the posterior end of the trunk. While one gets the impression that there are different sized muscles and different degrees of fusion, no pattern can be discerned. We are unable to suggest how this information can be universally applied even if species specificity was evident.

5. *Spindle muscle attachment.*—This thin muscle extends from the body wall at the posterior end of the trunk, through the gut coils, and along the rectum to the body wall just anterior to the anus. While there have been a few reports of this muscle merging with the body wall posterior to the anus, the only cases of this kind we have been able to confirm are in *A. laevis* and *A. coyi* in which the muscle sends a large branch to the mid-dorsal body wall posterior to the anus. It is not always easy to trace the course

Table 2.—Selected morphological attributes of *A. elegans* and *A. steenstrupii.*

Aspidosiphon elegans				*Aspidosiphon steenstrupii*			
Trunk length in mm	Retractor origin; % trunk	Nephridia length; % trunk	Nephridia attachment; % nephridium	Trunk length in mm	Retractor origin; % trunk	Nephridia length; % trunk	Nephridia attachment; % nephridium
6	83	75	89	7	71	42	67
7	86	70	95	7	79	57	75
7	—	57	95	10	75	50	50
8	63	63	99	11	82	45	75
9	67	50	99	11	73	99	67
10	70	60	67	12	75	50	67
10	70	70	93	12	75	99	99
11	82	64	99	14	79	54	75
14	86	57	88	15	77	50	—
15	60	67	50	15	80	60	56
15	80	40	83	15	73	67	50
16	63	53	85	15	73	60	50
16	81	63	99	17	82	41	71
16	88	88	95	19	79	58	50
17	76	35	99	19	68	47	67
17	65	65	82	19	84	47	90
19	79	58	86	20	85	75	40
19	74	47	99	21	76	57	—
21	90	52	64	22	77	68	50
22	86	86	95	24	71	42	75
23	78	57	99	25	80	48	58
25	84	60	67	26	81	69	50
32	78	56	99	27	70	81	99
				28	75	65	99
				33	79	67	50
				33	85	52	53
				34	85	50	50
				50	76	70	33
				50	80	54	75

of this muscle, especially in smaller worms or where the spindle muscle seems to merge with the wing muscle. Except for the above species, the muscle originates anterior to the anus and, therefore, in this genus, it is of limited usefulness as a diagnostic character.

6. *Fixing muscle number.*—In most sipunculan taxa fine thread-like muscles anchor some part of the anterior intestine to the body wall. The maximum number recorded in this genus is one and its presence (or absence) has been considered systematically important by some biologists. Our review of the literature reveals a lack of consistency on this point. Our own studies strongly suggest that either: A. Genetic polymorphism exists within populations or B. This fragile structure is placed where it can be easily damaged during dissection. While it may be true that some species totally lack this muscle and others usually have one, the possibility of any one worm deviating from the norm is too great to give weight to this character.

7. *Nephridia (length, attachment, level of nephridiopore).*—Both the nephrostome and the nephridiopores are located at the anterior end of the nephridia, a pair of tubular sac-like ventro-lateral organs. These open to the outside at the anterior end of the trunk. Three attributes have been recorded and are sometimes treated as diagnostic.

First is the position of the nephridiopores relative to the anus. In the literature most species of *A.* (*Aspidosiphon*) and a few *A.* (*Paraspidosiphon*) are reported as having nephridia at the level of the anus but slightly posterior to it in the remaining species. In this latter group our own data show this distance to be 3–8% of the trunk length. However, even in these populations a few animals have the nephridiopores and anus at the same level. While there do seem to be other species where this distance is almost always zero, careful examination of more than ten worms will probably reveal one or two where these openings are not at the same level. It may be possible to say: "80–90% of species X have these openings at the same level while in species Y only 5–10% do." But as these kinds of data are not always available (small sample sizes), the information has limited value to the systematist.

A second attribute is the length of these organs. The literature includes statements like "very long, long, reach to the base of the retractors, two-thirds/half/one fourth as long as the trunk," etc. Our observations show a range of lengths within a population, not correlated with trunk size (see Table 2), but there are some differences among species. Six species have nephridia half the trunk length or less. Many exhibit a broad range (e.g., 25–100%, 45–85%, 50–100%) and a few have only long nephridia (over 85% of the trunk length). With a few exceptions, nephridia length can only be used in a limited manner.

A third attribute often mentioned is the attachment of the nephridia to the body wall by a membranous sheet of connective tissue. Occasionally this takes the form of filamentous strands of tissue scattered along the nephridia that bind them less tightly. While nephridial attachment often appears in keys to *Aspidosiphon,* its constancy is overrated. While the original description may state that the nephridia are attached for a particular length (one-half, two-thirds, 100%, etc.), subsequent authors either ignore it or do not verify it critically. The connective tissue is easily torn, and within a single worm the attachment can differ for each organ. In most species a wide range of values is observed, commonly in the 50–100% range (see Table 2 for *A. steenstrupii,* 50–80% and *A. elegans,* 80–100%) while *A. muelleri* ranges from 0–100% attached in different reports. Therefore, this attribute has restricted systematic value.

8. Rectal caecum (presence, complexity).—In many sipunculans there is a small caecum on the rectum near the intestinal coil. Certain species of *Aspidosiphon* are reported to lack a caecum while others are said to have one. Two problems exist: If one looks at all of the published reports of any frequently recorded species, one finds inconsistencies, e.g., in *A. elegans* several authors say it lacks a caecum, others make no mention (this could mean that it is absent or possibly that they did not look for it), and a few report seeing the caecum. Alternatively, *A. muelleri* has been said to have a caecum by many authors but a few assert that it lacks one. In the *A. muelleri* we have recently examined, 25% have a caecum. In *A. albus* the original describer (Murina 1967c) asserts that the caecum is absent. Subsequent workers looking at other members of the population (Cutler 1973, Migotto & Ditadi 1988) saw one.

The second problem is related to this and it is illustrated by our finding a caecum in two of ten *A. elegans* we examined. Here we have one observer looking at one deme and finding dimorphism. In 30 worms that Migotto & Ditadi (1988) dissected they found a caecum in 18 (two of these being "large, villous"). In other words, 40% of this population of a species described as having a caecum was found to lack one. As this is true for one population, it may be true for all. We conclude that it is an error to consider the presence or absence of a rectal caecum as species specific.

In this genus there is one special case, i.e., a rectal structure described as: ". . . the last part of the rectum densely bordered with long villi-like structures" (Selenka et al. 1883 in *A. cumingii*) or "rectum with caecum plus many blind tubes attached to both sides" (Sato 1939 for *A. grandis*) or "rectum with a larger caecum, many lobed on both sides" (Selenka et al. 1883 in *A. klunzingeri*) or "rectal caecum with lappets" (Edmonds 1956 in *A. klunzingeri*) or "a large cluster of blind sacs as ramified intestinal appendages" (Wesenberg-Lund 1937 in *A. pachydermatus*). Only one specimen of *A. pachydermatus* and two of *A. grandis* (100, 70 and 100 mm trunks) exist. Of the 12 records of *A. klunzingeri* that include morphological comments, only the original material (3 worms) has this type of rectal elaboration. For subsequent authors, its absence seemed inconsequential. Similarly, in the nine reports of *A. cumingii* with morphological comments, only Selenka et al. (1883) record this structure in five worms (the words are used by other authors but only when referring to Selenka et al.). So, while these species supposedly have an elaborate rectum, several authors have used this name for animals lacking said structure. In museum collections, fewer than 10 worms exist (Baird's two have been lost) with this condition. The four worms in our 1985 Hawaii material that we are calling *A. laevis* have trunk lengths of 7, 10, 11 and 14 mm. The largest and the smallest bear a single structure with 6–8 short branches or lobes coming off each side. The 10 and 11 mm worms show small lobes, but the precise structure is less clear due to the fragility of the rectum. In our 1988 Venezuela collections we have five *A. laevis* (10–30 mm trunks), but none of these has a caecum of any kind. Migotto & Ditadi (1988) report large villous, simple and no caeca in a single population.

The question posed above reappears here: If an author did not mention this structure, does that mean it was not present? In those cases when an author specifically says that the complex caecum was not present, what significance does that have? Historically the position that this is insignificant and variable within a population has implicitly prevailed. Our recent data confirm that and suggest that *A. laevis* has the genetic potential (perhaps polygenic), but this potential is not always expressed, and when it is expressed it may be overlooked by an observer.

9. Intestinal coils (tightness).—In some other genera the number of gut coils has been used as a systematic character, but we have elsewhere shown this to be size dependent and not useful. In *Aspidosiphon* the interest is restricted to the nature of the coiling. In most species a regular, compact double helix is present, but *A. misakiensis* exhibits a loose, less regular helix (Fig. 4). This has also been reported by a few authors for *A. elegans.* The helix is maintained by the fine strands of muscle linking the coils to the axial spindle muscle. In those animals having a looser gut coil the linkage is not continuous and the strands may be longer.

10. Longitudinal muscle (bundles, anastomosing, fracturing).—The body wall of sipunculans has an internal layer of longitudinal muscle. In one subgenus (*A. Aspidosiphon*) this is an undivided sheet, almost. In the other subgenus (*A. Paraspidosiphon*) this layer is divided into separate bundles. However, it is not always a clear-cut dichotomy. Intermediate conditions of two general types exist.

First, ten putative species of *A.* (*Aspidosiphon*) have been described as having fracturing of the muscle layer in the anterior dorsal trunk. Commonly this is restricted to the area under the anal shield, but in some species the fractures continue out beyond these borders for a small (10–20% of the trunk length) but variable distance.

The second variation occurs in species of *A.* (*Paraspidosiphon*) where the longitudinal muscle bands are not distinct. The degree of variation is much greater than in other genera with these bundles. While several have distinct rarely anastomosing bundles,

Fig. 4. Intestinal coil of *A. misakiensis* showing irregular loose arrangement (A—anal shield, M—retractor muscle, N—nephridium, R—rectum). Scale line = 2 mm.

many exhibit a modest degree of anastomosing and others show frequent cross linkages. In these latter the layer appears like a continuous sheet that has split or fractured and not like distinct bundles (e.g., *A. fischeri*).

The number of muscle bands varies considerably within a population and within an individual (25–35 anteriorly and 15–25 posteriorly). It is difficult in a few cases, especially in small worms, to know whether one is looking at an *A.* (*Paraspidosiphon*) with much anastomosing of bundles or at an *A.* (*Aspidosiphon*) with some fracturing of a layer.

While this character state may be used for separating subgenera, it is neither species specific nor discriminating at that level. Since the subdivision of a continuous layer appears to be an homoplastic, apomorphic condition (Cutler & Gibbs 1985) it is possible that it has arisen more than once within this genus. Therefore, using it as the single attribute to separate subgenera may mask actual phylogenetic relationships.

11. Angle of introvert to trunk.—In most *Aspidosiphon* the extended introvert protrudes at an angle of 75–90° to the main axis of the trunk at the ventral edge of the anal shield. However, in at least three species, all with very weakly developed anal shields, this angle is reduced to 45–60°. While this is not broadly useful, it can help in these special cases.

Summary.—Two characters that have broad taxonomic usefulness are the hook and anal shield morphology. Four characters useful for separating the genus into different subsets are: (1) longitudinal muscle layer continuous or divided, (2) retractors originating in the most posterior 5% of the trunk or in the 70–80% range, (3) caudal shield developed or not, and (4) nephridia length (less than 50% of trunk length, more than 75%, or a broad range). An introvert/trunk angle of less than 75° separates three species, while a bifurcated anterior spindle muscle and a loosely wound gut coil each characterizes one species. The presence/absence of fixing muscles or caecum, the placement of the nephridiopores, and the attachment of the nephridia to the body wall are too variable to have any systematic value in this genus.

Systematic Section

Aspidosiphon Diesing, 1851

Diagnosis.—Introvert usually longer than trunk. Recurved hooks in numerous rings (absent in three, only scattered in two species). Trunk with anal shield composed of hardened units (occasionally inconspicuously developed). Introvert protrudes from ventral margin of shield. Body wall either with continuous longitudinal muscle layer or with longitudinal muscle layer gathered into anastomosing, sometimes ill-defined, bundles. Oral disk with tentacles enclosing dorsal nuchal organ but not mouth. Contractile vessel without villi. Two introvert retractor muscles sometimes almost completely fused. Spindle muscle attached posteriorly. Two nephridia. One species may exceed 100 mm but most less than 40 mm long.

We herein create a new subgenus for a set of five species as defined below. The major character state we focus on is the absence of compressed hooks in rings, a plesiomorphic character state for this entire class (Cutler & Gibbs 1985). One could argue that these species represent primitive transition forms from a very early ancestral stock, but we propose instead that this trait has been secondarily lost through subsequent evolution, i.e., a type of reversal. In support of this, note the atypical ecology of these taxa (e.g., interstitial or abyssal, none boring in coral or rock) suggesting an ecological specialization.

The following four taxa are not considered valid members of this genus and are discussed first. After the key, the remaining species are presented alphabetically within subgenera.

Aspidosiphon cylindricus Horst, 1899

Aspidosiphon cylindricus Horst, 1899:195–198, text-figs. 3–4.—Stephen & Edmonds, 1972:222–223.—Not Sluiter, 1902:18–19.

Material examined.—ZMUA, Sluiter's material (V. Si. 26.8).

Discussion.—This species was based on a single worm that disappeared from the Leiden museum prior to 1930 (van der Lund, pers. comm.). Enough questionable but now unverifiable features exist (especially the hook morphology) that we place this name on the list of *species inquirenda* pending future clarification. Sluiter's (1902) material was reexamined and is herein referred to *A. elegans.*

Aspidosiphon insularis (Lanchester, 1905)

Aspidosiphon insularis Lanchester, 1905b: 40, pl. 2, fig. 4.—Gibbs & Cutler, 1987: 56.

Paraspidosiphon insularis.—Stephen & Edmonds, 1972:247.

Material examined.—BMNH, type (1924.3.1.80).

Discussion.—This worm is in poor condition, but, as noted by Gibbs & Cutler (1987), it is clearly a *Phascolosoma* and based on hooks and papillae is a junior synonym of *P. perlucens.*

Aspidosiphon macer (Sluiter, 1891)

Phascolosoma macer Sluiter, 1891:114–115, pl. 2, figs. 13–14; 1902:34.
Golfingia macra.—Stephen & Edmonds, 1972:149.—Cutler & Murina, 1977:183.
Aspidosiphon macer.—Cutler & Cutler, 1986:568.

Material examined.—ZMUA, type and only specimen (V. Si. 65).

Discussion.—This putative taxon is based on a single specimen that has been thoroughly dissected over the years. The generic status is not altogether firm since the anal shield is very poorly developed and the introvert does not appear to be ventrally displaced. The gut is missing and while Sluiter asserted that the spindle muscle is not attached posteriorly, there is a muscle coming from the center of the caudal shield that we interpret as the broken posterior portion of this muscle. Sluiter said there were no hooks but there are about ten distinct rings of sharply pointed, unidentate hooks. The longitudinal muscle layer is undivided. While Sluiter asserted that the tentacles surround the mouth, the introvert is not extended so one cannot really tell how the tentacles are arranged. They appear to us to be clustered towards one side as in this genus. Therefore, until additional material is obtained to clarify this uncertainty, we place this name on the list of *species inquirenda.*

Golfingia mokyevskii Murina, 1964

Golfingia mokyevskii Murina, 1964a:256–259, figs. 4–5.
?*Aspidosiphon mokyevskii.*—Gibbs et al., 1983:302.

Material examined.—ZIAS, type material.

Discussion.—Gibbs et al. (1983) suggested that Murina's species might be an *Aspidosiphon*; however, it is now clear that this was an error. The 50 long tentacles, absence of hooks, anastomosing longitudinal muscle bands, large dark papillae at the base of the introvert, and especially the presence of contractile vessel villi all support placing this name in the synonymy of *Antillesoma antillarum.*

Key to *Aspidosiphon* species

1\. Hooks not present, or if present, not in rings .... *A.* (*Akrikos*) 2
– Hooks arranged in rings on distal portion of introvert 6
2\. Introvert hooks absent 3
– Scattered introvert hooks present 5
3\. Anal shield of tightly packed, uniform sized, pale, flat units with distinct angular margin *A. albus* Murina
– Anal shield of dispersed, often dark units, sometimes very poorly developed, with indistinct margin .. 4
4\. Anal shield units distinct, dark; those around margin usually pointed cones .... *A. venabulum* Selenka, de Man & Bülow
– Anal shield units indistinct, widely spaced, flat, sometimes arranged in indistinct rows .... *A. thomassini* Cutler & Cutler
5\. Anal shield ill defined and diffuse, trunk usually more than 5 mm, shallow warm water .... *A. mexicanus* Murina
– Anal shield well defined and compact, trunk usually less than 5 mm, deep cold water ..... *A. zinni* Cutler
6\. Longitudinal muscles in continuous layer (except under anal shield) .... *A.* (*Aspidosiphon*) 7
– Longitudinal muscle layer divided into separate (or anastomosing) bundles .. *A.* (*Paraspidosiphon*) .. 13
7\. Anal shield with extensive array of furrows present, not just around margin 8
– Anal shield with randomly distributed hardened units, lacking extensive grooves/furrows 9

8. Individual units form into longitudinal ridges over dorsal half of anal shield ...... *A. muelleri* Diesing
– Individual units arranged in offset squares or rectangles .... *A. spiralis* Sluiter
9. All hooks unidentate, ill-defined anal shield .... *A. gracilis* (Baird)
– Distal hooks bidentate, anal shield distinct 10
10. All compressed hooks bidentate followed by dark conical hooks ..... *A. elegans* Chamisso & Eysenhardt
– Distal bidentate compressed hooks followed by proximal unidentate ones 11
11. Interstitial, introvert 2–5 times the trunk length, nephridia 25–33% trunk .... *A. exiguus* Edmonds
– Occupies coral or shells often subtidal, introvert 1–3 times trunk, nephridia more than 50% of trunk length 12
12. Normal gut helix, lives in gastropod shells, anal shield units square, arranged in rows, and each made up of smaller granular subunits . ... *A. gosnoldi* Cutler
– Gut coils loose or absent, does not occupy gastropod shells, anal shield units more solid and randomly arranged .... *A. misakiensis* Ikeda
13. Anal shield ungrooved or, if present, only as short marginal ones (Fig. 5A) 14
– Anal shield with extensive grooves or furrows present (Fig. 5B) 18
14. Distal hooks bidentate 15
– All hooks unidentate .... *A. planoscutatus* Murina
15. Compressed hooks bidentate followed by dark pyramidal hooks . ... *A. steenstrupii* Diesing
– Compressed hooks of both types, pyramidal hooks pale, if present 16
16. No pyramidal hooks, longitudinal muscle bands distinct, compressed hooks over 30 μm tall, retractor origins 75–88% ..... *A. tenuis* Sluiter
– Pale pyramidal hooks present, longitudinal muscle bands indistinct, hooks less than 30 μm tall, retractor origins 95–100% 17
17. Anal shield marginally becomes diffuse forming cones or spikes, nephridia more than ½ trunk ... . *A. parvulus* Gerould
– Anal shield with distinct margins, no cones or spikes, nephridia less than ½ trunk ... *A. fischeri* ten Brocke
18. All hooks unidentate, retractor origins not at posterior end (60–80%) .... *A. laevis* Quatrefages
– Distal hooks usually have very small secondary tooth, retractor origins at posterior end (95–100%) .... *A. coyi* Quatrefages

Aspidosiphon (*Akrikos*), new subgenus

Diagnosis.—*Aspidosiphon* with compressed hooks not in rings, i.e., either scattered and small (less than 30 μm), or absent; caudal shield absent or very diffuse; longitudinal muscle layer continuous. Not known to bore in coral or rock.

The name is from the Greek meaning "without rings." The spelling is a literal transliteration according to the classical method.

Type species: *Aspidosiphon albus* Murina, 1967.

Aspidosiphon albus Murina, 1967

Aspidosiphon albus Murina, 1967a:1330–1331, fig. 2 (1)–(3).—Stephen & Edmonds, 1972:219–221.—Cutler, 1973: 174–175.—Cutler & Cutler, 1980a:4.—Migotto & Ditadi, 1988:247–248.—Not Cutler et al., 1984:307.

Aspidosiphon hartmeyeri.—Wesenberg-Lund, 1957a:7–8; 1959a:197; 1959b:212.

Material examined.—ZIAS, type; USNM, cataloged as *A. cumingii* 066214-222 off Louisiana; material from Brazil (Cutler &

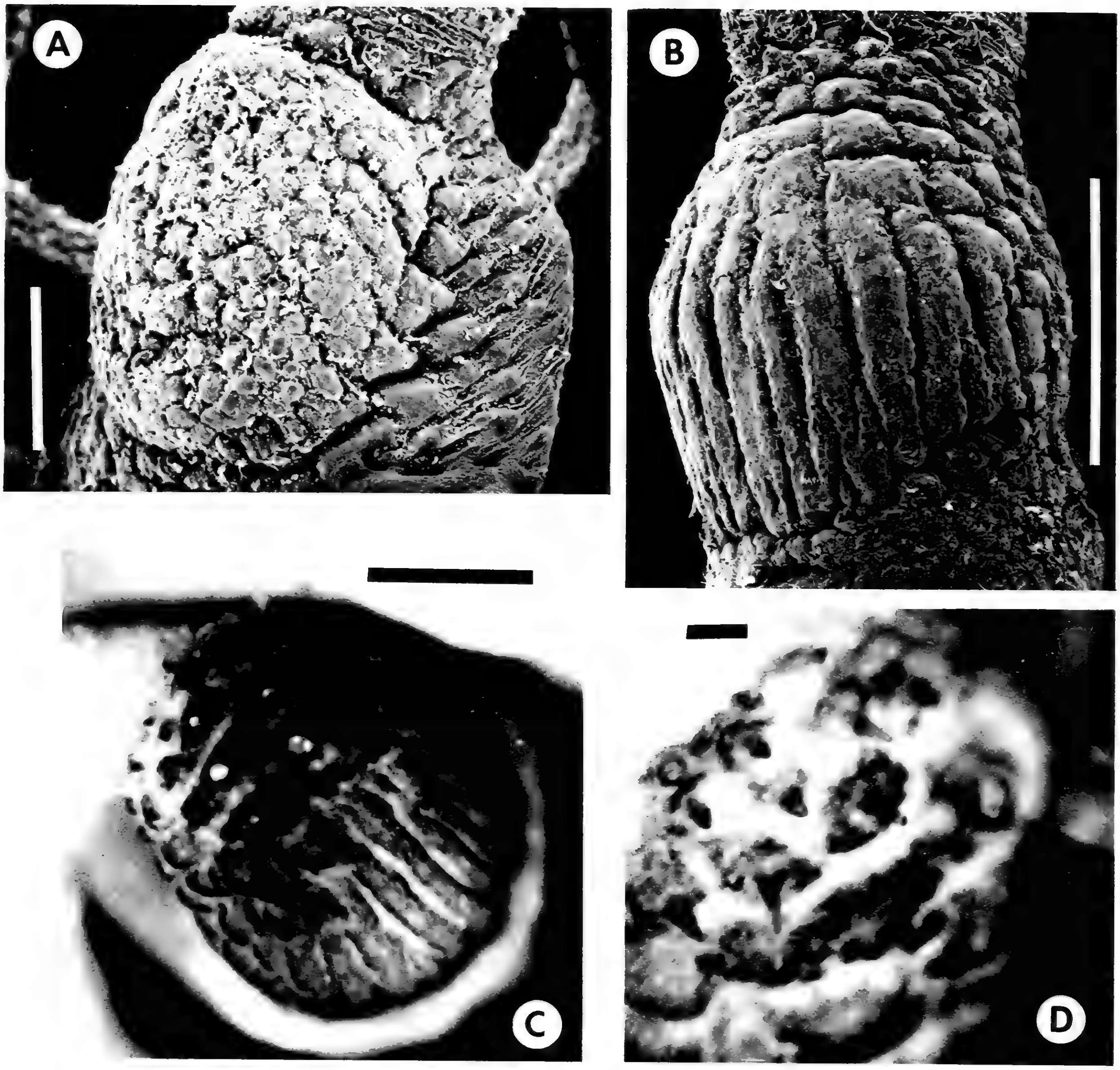

Fig. 5. Anal shields: A, Ungrooved type of *A. elegans*; B–C, Grooved type as in *A. muelleri*; D, Ventral cone-shaped units near the ventral margin present in some *A. muelleri*. Scale lines on A, B, C = 0.5 mm, D = 0.1 mm.

Cutler 1980a), U.S. east coast (Cutler 1973), and new Ivory Coast material from 5°N, 4°W, at 20 m; *A. hartmeyeri,* UZMK, Wesenberg-Lund's Niger worms.

Discussion.—This hookless species also seems to lack tentacles. The recorded body length ranges from 2 to 45 mm, the introvert is 3–5 times the trunk length, and the anal shield is fine grained with small furrows around the margin but without grooves. Often there is a median stripe made up of darker units. The nephridia are 50–75% of the trunk.

The Cutler et al. (1984) record was based on one incomplete worm and was not a positive identification. This should not be included within this species unless additional material is found in Japanese waters.

Distribution.—Cape Hatteras, northern Gulf of Mexico (unpublished), Cuba, Brazil continental shelf (10–123 m), and the east Atlantic from the Gulf of Guinea. It is the most common member of this genus on the Brazilian shelf.

Aspidosiphon mexicanus (Murina, 1967)

Golfingia mexicana Murina, 1967c:1333–1334, fig. 3.

Aspidosiphon mexicana Cutler et al., 1983: 673.
Aspidosiphon longirhyncus Cutler & Cutler, 1980a:4–6, figs. 4–5.

Material examined.—ZIAS, type; *A. longirhyncus,* AMNH, type (4022); other material of both species from the type localities. Also, 12 unpublished specimens from the Azores (33°N, 16°W, 320 m) and seven from three stations off Florida and North Carolina (25–34°N, 85–190 m).

Discussion.—This species does not have the typical aspidosiphonid appearance in that the anal shield is very weakly developed with scattered, ill-defined platelets. Also, the introvert is on an atypical angle (45–60°) with the main trunk axis. The caudal shield is almost nonexistent. The introvert is 4–5 times the trunk length, bearing scattered, small (less than 30 μm), unidentate compressed hooks. The nephridia are 35–75% of the trunk.

The decision to combine these two names was discussed in Cutler et al. (1983) as part of a review of the taxon containing Murina's species.

Distribution.—Southern Brazil, Cuba, and southeastern U.S. at shelf depths (80–200 m), and the Azores at 320 m.

Aspidosiphon thomassini Cutler & Cutler, 1979

Aspidosiphon thomassini Cutler & Cutler, 1979a:971–973, figs. 3–14.

Material examined.—MNHN, type material (AH 406–408).

Discussion.—This is another small (1.5–7 mm) hookless species whose tentacles (if present) have yet to be observed. The retractor muscles are fused for most of their length and the nephridia are around 50% of the trunk. The introvert is 2–4 times the trunk length. These have no caudal shield and the anal shield is very poorly developed. This, together with the smaller angle between the trunk and introvert axis (40–45°) make it possible to mistakenly identify this as a *Nephasoma* species.

Distribution.—Intertidal coral sands in Madagascar and French Polynesia.

Aspidosiphon venabulum Selenka, de Man & Bülow, 1883

Aspidosiphon venabulum Selenka et al., 1883:123, pl. 14, figs. 202–204.—Fischer, 1895:18; 1914a:68–69.—Wesenberg-Lund, 1957c:5–7; 1959a:196–197; 1959c: 212.—Longhurst, 1958:85.—Stephen, 1960a:519.—Cutler, 1977a:148.
Aspidosiphon venabulus.—Stephen & Edmonds, 1972:237.—Cutler & Cutler, 1979a:971.

Material examined.—MNHU, type (644); UZMK, Wesenberg-Lund's Atlantide material; worms from Madagascar (Cutler & Cutler 1979a) and West Africa (Cutler 1977a).

Discussion.—This species lacks hooks and the anal shield is ungrooved, being made up of dark, pointed, conical units more widely scattered than in many species. It resembles the anterior end of certain *Phascolion* species that have large anterior papillae. The retractor muscles extend to the posterior end and under the anal shield, the longitudinal muscle layer splits into a few bundles. The nephridia are 60–95% of the trunk, the latter being reported from 5–30 mm.

Distribution.—Subtidal depths (10–55 m with one intertidal report and one at 960 m). Most records are off West Africa with one report from southern Madagascar.

Aspidosiphon zinni Cutler, 1969

Aspidosiphon zinni Cutler, 1969:209–211, fig. 1.—Cutler, 1973:176–178.—Cutler & Cutler, 1979a:968; 1980b:457; 1987a:73.

Material examined.—USNM, type material (38242, 38243); Atlantic Ocean material (Cutler & Cutler 1987a).

Distribution.—This small (most less than 5 mm), deep-water worm commonly lives in foraminiferan tubes. The anal shield is made up of very fine grained, pale units and the caudal shield is nonexistent. The small

(15–20 μm), scattered, unidentate, compressed hooks and introvert not longer than the trunk are unusual in this genus. The nephridia are less than 25% of the trunk.

Distribution.—Common in north Atlantic Ocean (1100–4400 m), two stations around 9°S off the Congo River (1535 and 2700 m), and one in the Mozambique Channel (25°S) at 132 m.

Subgenus *Aspidosiphon* (*Aspidosiphon*)

Diagnosis.—Introvert with compressed hooks in rings, longitudinal muscle layer continuous except near anal shield. Most do not bore in coral or rock.

Aspidosiphon elegans
(Chamisso & Eysenhardt, 1821)

Sternaspis elegans Chamisso & Eysenhardt, 1821:351–352, pl. 24, figs. 5a–e.
Sipunculus elegans.—de Blainville, 1827, pl. 26, fig. 2.
Loxosiphon elegans.—Diesing, 1851:70.—Quatrefages, 1865:605.
Phascolosoma (*Aspidosiphon*) *elegans.*—Grübe, 1868a:645–647.
Aspidosiphon elegans.—Selenka et al., 1883: 124–126.—Shipley, 1898:471; 1899b: 153.—Whitelegge, 1899:393.—Sluiter, 1891:116; 1902:19.—Hérubel, 1904: 564.—Lanchester, 1905a:33; 1905b:40.—Fischer, 1914b:14.—Gravely, 1927:87.—Sato, 1935:316; 1939:426–427.—Wesenberg-Lung, 1954:10–11; 1957a:198–199; 1957b:7–8; 1959c:68.—Cutler, 1977b:154.—Cutler & Cutler, 1979a: 968.—Edmonds, 1980:44–46.—Cutler et al., 1984:304.—Migotto & Ditadi, 1988: 248–250.
Aspidosiphon elegans elegans.—Stephen & Edmonds, 1972:223.
Aspidosiphon elegans var. *yapense* Sato, 1935:316–318, pl. 4, fig. 18, text-figs. 12–15.
Aspidosiphon elegans yapensis.—Stephen & Edmonds, 1972:224.
Aspidosiphon brocki Augener, 1903:328–330, figs. 9–13.—Murina, 1967b:42.—Rice, 1970:1618–1620; 1975:44–45.—Stephen & Edmonds, 1972:221.—Rice & Macintyre, 1979:311–319.
Aspidosiphon carolinus Sato, 1935:318–319, pl. 4, fig. 19, text-figs. 16–17.—Stephens & Edmonds, 1972:222.—Cutler & Cutler, 1981:77–78.
Aspidosiphon cylindricus.—Sluiter, 1902: 18–19.
Aspidosiphon exilis Sluiter, 1886:497, pl. 3, figs. 11–12; 1891:116; 1902:18.—Leroy, 1942:39–40.—Stephen & Edmonds, 1972: 224–225.—Edmonds, 1980:44–46.
Aspidosiphon homomyarium Johnson, 1964: 332–334, pl. 8.
Aspidosiphon homomyarius.—Stephen & Edmonds, 1972:227.
Aspidosiphon ravus Sluiter, 1886:495–496, pl. 3, figs. 9–10; 1891:116; 1902:18.—Shipley, 1899a:56; 1899b:153.—Stephen & Edmonds, 1972:234.
Aspidosiphon spinalis Ikeda, 1904:47–49, text-figs. 12, 81–85; 1924:37.—Sato, 1939:428.—Stephen & Edmonds, 1972: 234–235.—Cutler & Cutler, 1981:79–81.
Aspidosiphon spinosus Sluiter, 1902:28, pl. 2, figs. 17–19.—Stephen & Edmonds, 1972:235.

Material examined.—ZMUA, Sluiter's from Indonesia (V. Si. 3); worms from the western Pacific Ocean (Cutler et al. 1984), 1988 collections from the southern Caribbean, a few from Brazil (Migotto & Ditadi 1988); *A. brocki,* MNHU, type material (6954-5); USNM, Caribbean material identified by M. Rice (USNM 48924-5); *A. cylindricus,* ZMUA, two of Sluiter's (26.8); *A. exilis,* BMNH and ZMUA (V. Si. 4), parts of type material in both places, all of it badly dried out; *A. homomyarius,* RSME, two worms from India presumably deposited by Johnson (1965.32.1); *A. ravus,* ZMUA (V. Si. 13) and BMNH, type material.

Discussion.—Like *A.* (*Paraspidosiphon*) *steenstrupii* in its subgenus, *A. elegans* is the most common and widespread tropical member of this subgenus with many junior synonyms. Additionally, both species have ungrooved anal shields, bidentate compressed hooks in rings, and dark scattered hooks. Edmonds (1980:44–45) presented a detailed description of *A. elegans* and some interesting comments on this complex of related (or identical) taxa. What he illustrates as introvert spines (his figs. 77–78) are, by our definition, conical hooks. The variation in the shape (real and due to orientation on slide) of the bidentate hooks has led to the creation of different species. Figure 6 illustrates some of this variation (degree the hook is bent and sharpness of the point) that we now know to be within-deme variation. Six to twelve short stubby nuchal tentacles are present. The caudal shield is weakly developed, barely discernable in many worms.

Internally the longitudinal muscle layer may subdivide in the area of the anal shield. Less than 20% of the worms dissected have a caecum and a fixing muscle was seen in only 4% of the worms dissected. The nephridia open at the level of the anus or just posterior to it. Table 2 shows our observations on the nephridia and retractor origins. The gut has the normal helical coil, but about half the worms show a degree of looseness in part of the coil.

The putative species *A. carolinus* and *A. spinalis* were reduced to junior synonyms by Cutler & Cutler (1981) and *A. exilis* by Edmonds (1980). We reaffirm those decisions.

Aspidosiphon brocki (Augener 1903) is a name used by only two authors since it was described: Murina (1967b) and Rice (1970, 1975). Neither of these authors has used the name *A. elegans* in their writings. Augener's paper was the first of only two articles he wrote about this phylum, and he made no reference to any other member of this subgenus nor was there a differential diagnosis. The original report was from Malaya but the four subsequent records are all Caribbean, and all of this latter material is less than 10 mm long. Our recent Caribbean collections (340 worms) ranged from 4 to 22 mm long. The pictures of hooks in Stephen & Edmonds (1972:230, fig. 27B, F, G) illustrate the extremes of a continuum and could be misleading. This much variation occurs within demes. Comparison of the type, Rice's material, and our own Caribbean and Pacific material convinces us that this putative species is conspecific with *A. elegans*.

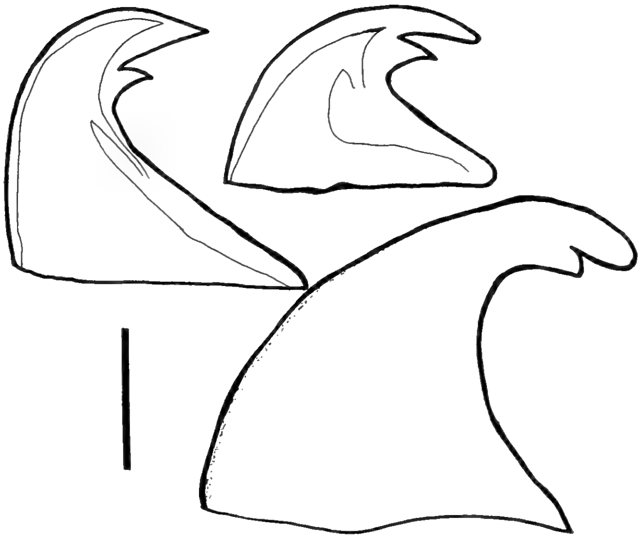

Fig. 6. Variation in shape of bidentate compressed hooks within a single specimen of *A. elegans*. Note difference in degree of bend and sharpness of point. Scale line = 20 μm.

Rice (1970) reported asexual reproduction by budding in *A. brocki*, something not recorded elsewhere in this phylum. Our Caribbean material showed this (even in 4 mm worms), but it is also present in our collections from Majuro, Marshall Islands, and in French Polynesian worms collected by Peyrot-Clausade.

Sluiter's (1902) *Siboga* report included *A. cylindricus*, Horst, but not *A. elegans*. Our examination of his material showed no differences from *A. elegans*.

When Johnson (1964) described *A. homomyarius*, he did not include a differential diagnosis except to contrast it with the other new species in that paper, so we do not know how he thought it differed from *A. elegans*.

He seemed to think that the dorsal array of nuchal tentacles was unique in this genus. Our examination of his two worms in Edinburgh confirmed our analysis of his article, i.e., meaningful differences from *A. elegans* are lacking.

Aspidosiphon ravus was described by Sluiter (1886) as having unidentate hooks. Our reexamination of the material (the Amsterdam worms are in good condition but the London worm is not) revealed bidentate compressed and conical hooks. The introvert is retracted in all three worms. This material is clearly conspecific.

Aspidosiphon spinosus Sluiter, 1902, was based on a single worm that has subsequently been lost. His description is indistinguishable from *A. elegans.* He compared it to *A. exilis* differentiating it by the form of the hooks and a few other features. Placing this name on the list of *incertae sedis* was considered since it cannot be examined (the hypothesis cannot be tested) but reducing it to a junior synonym of this species is a rational alternative given what we now know about within-deme variation.

The subspecies *A. elegans yapensis,* which Sato (1935) described as a variety, was differentiated on the basis of hook morphology: sharply pointed apex, not blunt. The within-deme variation we find makes it clear that this subspecies lacks biological significance.

Distribution.—Widespread and common in the Indian and western Pacific Ocean (from southern Japan to northern Australia out to Hawaii); the Red Sea and Israel. In the Caribbean from northern Brazil to the Florida keys and Bermuda.

Aspidosiphon exiguus Edmonds, 1974

Aspidosiphon exiguus Edmonds, 1974:187–192, figs. 1–7.

Material examined.—BMNH, holotype (1975.22.1).

Discussion.—The largest worm reported is less than 4.5 mm long, but it does bear bidentate hooks in rings as well as a few scattered unidentate compressed hooks. The introvert is very long (2–5 times the trunk) and no tentacles or gametes have yet been observed. The anal shield consists of small, pale units with no grooves. At the anterior/ventral border 1–4 cone-like papillae are present. It is similar to *A. albus* but has hooks and shorter nephridia (25–33%). In the anterior 10% of the trunk the longitudinal muscle layer is divided into bands visible through the body wall. *Aspidosiphon* (*Paraspidosiphon*) *parvulus* is common in this area and is similar in several ways despite having longitudinal muscle bands (weakly developed).

Distribution.—Cuba, intertidal, interstitial.

Aspidosiphon gosnoldi Cutler, 1981

Aspidosiphon gosnoldi Cutler, 1981:445–449, figs. 1–4.—Migotto & Ditadi, 1988: 253–254.

Aspidosiphon spinalis.—Cutler, 1973:175–176.—Cutler & Cutler, 1979b:107.

Material examined.—USNM, type (61624-5) and additional material from the western Atlantic Ocean (Cutler 1981).

Discussion.—The anal shield is composed of randomly arranged flat units of relatively uniform size. The borders are usually distinct but dark skin papillae may be present at the anterior end of the trunk. The introvert is 1.5–3 times the trunk length and bears distal rings of 20–30 μm, bidentate hooks (the secondary tooth may be small). Scattered, pale, pyramidal hooks cover much of the proximal part of the introvert. This is in the group of species where the longitudinal musculature commonly splits into irregular bundles under the anal shield and the retractors originate from the caudal shield. The intestine forms a normal helical coil, and the nephridia are 50–90% of the trunk length.

Distribution.—Shelf waters (7–185 m) from Cape Hatteras to Florida and Brazil (to 23°S) living in gastropod shells.

Aspidosiphon gracilis gracilis (Baird, 1868)

Pseudoaspidosiphon gracile Baird, 1868:103, pl. 10, figs. 1, 1a.

Aspidosiphon gracilis—Selenka et al., 1883: 122–123.—Sluiter, 1902:17.—Augener, 1903:319–321.—Hérubel, 1904:564.—Rice & Stephen, 1970:69.—Stephen & Edmonds, 1972:225–226.—Gibbs, 1978: 85.—Edmonds, 1980:46–47.

Material examined.—BMNH, syntypes (43.5.15.58a/b); MNHN, two of Hérubel's specimens (V20).

Discussion.—This species has an underdeveloped anal shield composed of noncontiguous brown papillae surrounded by darker platelets. These units are arranged in irregular longitudinal rows. The introvert comes off at about a 60° angle, is up to 1.5 times the trunk length, and the slender trunk (up to 15 times the width) is coarsely papillated all over. The assertion that bidentate hooks are present (Stephen & Edmonds 1972) must be a flawed translation since we cannot find any other reference to them. The unidentate hooks are in rings, are broader than high (up to 40 μm), and are followed by a proximal area of pyramidal hooks. The retractor muscles originate very near the posterior end and the nephridia are as long as the trunk.

Hérubel (1904) had three worms from the Gulf of Aden that look different but are damaged and desiccated such that we cannot confirm or refute his identification.

Distribution.—Australia, Indonesia, Philippines, Gulf of Aden and an unpublished record from the Andaman Islands.

Aspidosiphon gracilis schnehageni Fischer, 1913, new status

Aspidosiphon schnehageni Fischer, 1913:99–100, figs. 4–6; 1914b:15.—Wesenberg-Lund, 1955:13.—Ditadi, 1975:200–202.

Paraspidosiphon schnehageni.—Stephen & Edmonds, 1972:252.

Material examined.—ZMUH, type specimen (V2127).

Discussion.—The type specimen is in very poor condition, missing, among other parts, the distal end of the introvert and the retractor muscles. Ditadi (1975) redescribed this taxon, but his material cannot be located at the Los Angeles County Museum or the Hancock Foundation where it had been deposited. The anal shield was described as furrowed by Fischer but as randomly arranged plates by Ditadi. This is another situation where the units may sometimes appear arranged in rows giving an impression of indistinct ridges and furrows. The longitudinal musculature is partially separated into 10–14 anastomosing bundles in the anterior part but is continuous elsewhere. In this regard, it is one of the borderline taxa not having distinct bundles, and, therefore, we have moved it into this subgenus.

The decision to reduce this to a subspecies rather than a junior synonym was based on ill-defined differences from the nominate form; habitat (mollusc shells), hook shape (more triangular), nephridia (shorter, 33–50%), trunk size and shape (length less than 8 times the width), and longitudinal muscle layer (splitting extends beyond the anal shield). These are not clear or distinct differences by themselves, but if one adds the geographical gap between the populations (most of the Pacific Ocean), this status may be appropriate pending additional material for better comparison. The west coast of Central and South America are very poorly represented in curated, accessible collections.

Distribution.—Chile and Pacific coast of Guatemala.

Aspidosiphon misakiensis Ikeda, 1904

Aspidosiphon misakiensis Ikeda, 1904:41–43, text-figs. 9, 68–72.—Sato, 1939:428.—Stephen & Edmonds, 1972:229–231.—Cutler & Cutler, 1981:78–79.—Cutler et al., 1984:305–306.

Aspidosiphon hartmeyeri Fischer, 1919:281–282, text-figs. 1–3; 1926:204–205.—Edmonds, 1956:306–307; 1980:47.—Murina, 1967c:1332.—Stephen & Edmonds, 1972:226–227.—Cutler, 1977a:147–148. Not Wesenberg-Lund, 1957a:7–8; 1959a:197; 1959b:212.

Aspidosiphon gerouldi ten Broeke, 1925:93, text-figs. 23–25.—Stephen & Edmonds, 1972:225.—Cutler & Cutler, 1979b:106–107.—Migotto & Ditadi, 1988:251–253.

Aspidosiphon speculator.—Saiz Salinas, 1986a:11–14.

Material examined.—USNM, paraneotype; other material from the type locality (Cutler & Cutler 1981); *A. gerouldi,* ZMUA, type (V. Si. 7), material from Azores (Cutler & Cutler 1987), and Brazil (Migotto & Ditadi 1988); *A. hartmeyeri,* ZMUH (V8913-14) and MNHU (6036), co-types; UZMK, Wesenberg-Lund's Niger material (=*A. albus*); *A. speculator,* three specimens identified by Saiz Salinas.

Discussion.—The anal shield is composed of closely packed, irregular, granular units, but it has borders that are not sharply defined, i.e., widely spaced, square blocks of shield material are around the anterior quarter of the trunk. The caudal shield is granular but does have vague radial grooves present. Bidentate hooks are present (25–40 μm) in distal rings, then proximally the hooks are scattered, unidentate compressed, 25–60 μm tall (Fig. 1B). The secondary tooth has normal dimensions on distal hooks but becomes very small in proximal ones. The introvert is up to three times the trunk length (largest known worm is 25 mm). The longitudinal muscle layer exhibits some fractures/splits in some individuals, and the gut coils are ill defined or only loosely wound. In 6–7 mm worms the intestine has a few loose folds, is anchored at the posterior end, then has a straight tube to the anus. Sheets of connective tissue link the ascending and descending loops. The nephridia are 50–100% of the trunk and the retractors originate very close to the caudal shield.

When Fischer (1919) described *A. hartmeyeri* from Australia, he made no reference to Ikeda's *A. misakiensis* even though it is clear he knew of Ikeda's paper. Stephen & Edmonds' (1972) key uses the nephridia being mostly free to separate it from Ikeda's. Our examination of five type specimens showed considerable variation (up to 80% attached and length up to 100% of the trunk, not 0% and 50% as stated). The anal shield was described as having 5–6 flat grooves. These are not grooves but irregular units arranged in indistinct rows in a few worms (see also Edmonds 1956:306). Wesenberg-Lund's four worms from West Africa are clearly part of the *A. albus* population. She never recorded hooks, and her drawings of one, plus our examination of another, confirm this.

The decision to reduce the status of *A. gerouldi* came after examination of unpublished material from the Azores and comparison to the Japanese worms. The original description was based on a single worm, but several hundred have been subsequently collected. The bidentate hooks in the Azores population are at the small end of the range (25–30 μm) as is the introvert (only up to twice the trunk in worms up to 20 mm long).

Saiz Salinas (1986a) used the name *A. speculator* for 18 worms off Spain and the Canary Islands. This population is particularly troublesome as indicated by his placing it in *A.* (*Paraspidosiphon*). The longitudinal musculature is neither continuous nor divided into distinct bands. It varies from worm to worm in degree, but we interpret it to be continuous with fracturing in the anterior part, especially on the dorsal side. In other respects (hooks, shield, gut) his worms fit *A. misakiensis* better than any other taxon.

Distribution.—In the Pacific from both sides of central Japan at 1–50 m depth, South and West Australia, and Kermadec Island. In the eastern Atlantic from the Azores, Cape Verde, and Canary Islands to the Gulf of Guinea, at depths down to 75 m, and the Spanish Mediterranean. In the western Atlantic from Brazil (14–16°N), Haiti, and Cuba.

Aspidosiphon muelleri Diesing, 1851

Aspidosiphon muelleri Diesing, 1851:68.—Quatrefages, 1865:609–610.—Schmidt, 1865:56–66.—Baird, 1868:101.—Selenka et al., 1883:120–121.—Fischer, 1895: 18; 1914a:69–70; 1914b:13–14; 1922a:22–23; 1925:25–26.—Sluiter, 1900:14; 1902: 18; 1912:19.—Hérubel, 1904:564.—Southern, 1912:31–34.—J. Fischer, 1914: 105–106.—Ikeda, 1924:38.—Stephen, 1934:173; 1941:257; 1958:133–134; 1960a:518–519; 1960b:22–23.—Steuer, 1936:5; 1939:2.—Sato, 1939:428.—Chapman, 1955:351.—Wesenberg-Lund, 1957a:4–5; 1957b:197–198; 1959a:194–196; 1959c:68.—Longhurst, 1958:1.—Stephen & Edmonds, 1972:231–233.—Zavodnik & Murina, 1975:127; 1976:81–82.—Cutler, 1977a:148.—Gibbs, 1977: 30–31.—Cutler & Cutler, 1979b:107; 1987a:73.—Ocharan, 1980:114–115.—Cutler et al., 1984:306–307.—Saiz Salinas, 1984:177–178; 1986a:9–11.

Sipunculus scutatus J. Müller, 1844:166–168 (not *scutatum* J. Müller, 1843).—Keferstein, 1867:52.—Selenka et al., 1883:120.

Phascolosoma scutatum.—Krohn, 1851: 371.—Selenka et al., 1883:120.

Aspidosiphon clavatus.—Diesing, 1851: 68.—Cuénot, 1922:12–13.—Hérubel, 1924:111.—Leroy, 1936:426.—Åkesson, 1958:206.—Voss-Foucart et al., 1977: 135.

Pseudaspidosiphon clavatum.—Baird, 1868: 103.

Sipunculus cochlearius Valenciennes, 1854: 640.—Saiz Salinas, 1986b:554.

Lesinia farcimen Schmidt, 1854:2.—Selenka et al., 1883:120.

Aspidosiphon eremita Diesing, 1859:768 (not *Phascolosoma eremita* Sars, 1851).

Phascolosoma radiata Alder, 1860:75.—Southern, 1913:32.

Sipunculus heterocyathi McDonald, 1862: 78–81.—Saiz Salinas, 1986b:554.

Aspidosiphon jukesii Baird, 1873:97.—Rice & Stephen, 1970:68–69.—Stephen & Edmonds, 1972:228.—Cutler & Cutler, 1979a:969–970.—Edmonds, 1980:49.—Saiz Salinas, 1986b:551.

Aspidosiphon mirabilis Théel, 1875:17; 1905:91–92.—Selenka et al., 1883:121.—Southern, 1913:31–33.

Aspidosiphon armatum Danielssen & Koren, 1880:464; 1881:64.—Selenka et al., 1883:124.—Théel, 1905:93.—Southern, 1913:31–33.

Aspidosiphon tortus Selenka et al., 1883:119–120, pl. 14, figs. 196–201.—Hérubel, 1904:564.—Fischer, 1923:21–22.—Stephen & Edmonds, 1972:236–237.—Gibbs, 1978:85.

Aspidosiphon heteropsammiarum Bovier, 1894:98.—Saiz Salinas, 1986b:555–557.

Aspidosiphon michelini Bovier, 1894:98.—Saiz Salinas, 1986b:557–559.

Aspidosiphon corallicola Sluiter, 1902: 19–22.—Shipley, 1903:169–171.—Stephen & Robertson, 1952:441–442.—Cutler, 1965:58.

Aspidosiphon imbellis Sluiter, 1902:29, pl. 2, fig. 20.—Stephen & Edmonds, 1972: 227–228.

Aspidosiphon inquilinus Sluiter, 1902:29–30, pl. 2, figs. 21–22.—Stephen & Edmonds, 1972:227.—Edmonds, 1980:47–49.

Aspidosiphon exhaustum Sluiter, 1912:20–21, pl. 1, fig. 11.—Murina, 1971:78.

Aspidosiphon exhaustus.—Stephen & Edmonds, 1972:224.—Murina, 1972:295–296; 1978:120.—Cutler & Cutler, 1979a: 969; 1980a:4.—Edmonds, 1980:46.—Cutler et al., 1984:305.

Aspidosiphon exhaustus mirus Murina, 1974:1715–1716, fig. 2.

Aspidosiphon pygmaeus Fischer, 1921:45–47, text-figs. 1–7.—Murina, 1967a:54; 1971:78.

Paraspidosiphon pygmaeus.—Stephen & Edmonds, 1972:251–252.

Aspidosiphon kovaleskii Murina, 1964b:51–55, figs. 1–5; 1970:66.—Stephen & Edmonds, 1972:229.—Zavodnik & Murina, 1975:127.—Cutler & Cutler, 1979a:970–971.

Aspidosiphon hispitrofus LiGreci, 1980:123–134, figs. 1–4.

Material examined.—ZMUA, Sluiter's Indonesian worm (V. Si. 253); material from the Azores, 1–600 m depth collected by Zibrowius and CENTOB; Celtic Sea from P. Gibbs; French Mediterranean from Voss-Fouchart; Japan (Cutler, Cutler & Nishikawa 1984); *A. armatus,* ZMUB, type (1745); *A. corallicola,* ZMUA, types (V. Si. 1); *A. exhaustus,* MOMV, type; Cutlers' Brazilian, Japanese and Indian Ocean worms; *A. imbellis,* ZMUA, type (V. Si. 25/5); *A. inquilinis,* ZMUA, type (V. Si. 25/6); *A. jukesii,* BMNH, type (1965.25.3); Indian Ocean material (Cutler & Cutler 1979a); *A. kovaleskii,* ZIAS, type; Indian Ocean worms (Cutler & Cutler 1979a); *A. mirabilis,* ZMUB, type (15957); *A. pygmaeus,* NHRS, type specimens (279).

Discussion.—This species is the widespread, eurytopic, polymorphic member of this genus and in this way is comparable to *Golfingia margaritacea, Phascolion strombus, Sipunculus nudus,* etc. Each genus seems to have one such species with a long list of junior synonyms and a morphology difficult to define with precision. Stephen & Edmonds (1972:232–233) discuss some of the early confusion about the proper name for this taxon. Most records are from the north Atlantic Ocean and Mediterranean Sea from abandoned mollusc shells. When biologists found similar worms from different parts of the world or from different habitats, new names were put forth.

Our present concept of *A. muelleri* has an anal shield made up of very small units arranged into variable sized plates, partially separated by longitudinal furrows dorsally, in the midsection by transverse furrows, and made up of raised wart-like or cone-shaped units ventrally (Fig. 5C). The possibility that two species exist, one with pointed, cone-shaped spines on the ventral part of the anal shield and the other with only flat wart-like units, was considered. It is our conclusion that this species has the capability to respond to some environmental stimulus (e.g., pressure, temperature, or host shell shape), or that random allelic frequency shifts can occur, to produce anal shields with ventral units varying in degree of cone development.

The trunk may be straight or coiled depending on its habitat. The introvert is 1–3 times the trunk length, and there are 6–12 small nuchal tentacles. Hook morphology has been a long standing point of confusion (see Southern 1913, Stephen & Edmonds 1972:233). Our analysis of within-deme variation of compressed hooks clearly suggests that *A. muelleri* has the genetic potential for producing only unidentate hooks or only bidentate hooks or some of both on a single worm. Proximal to the rings (covering about one-third of the introvert), the scattered hooks quickly change from compressed unidentate to pyramidal. The SEM photomicrographs reveal the existence of small comb-like structures at the posterior base of the compressed hooks (Fig. 1A).

Internally the pair of introvert retractor muscles originates from the edge of the caudal shield. Under the anal shield the longitudinal muscle layer divides into separate bands. The nephridia open at or just posterior to the anus, are from 25–100% of the trunk length, and the gut forms a regular helical coil. The rectal caecum and fixing muscle are only present in some individuals.

Aspidosiphon jukesii (Baird 1873) and its several junior synonyms must be moved into this species. When one considers each character and looks not just at one author's perception but at the collected writings and the many specimens at hand, the presumed "bridgeless gap" ceases to exist. If a young worm occupies a gastropod shell in an area where solitary corals live, it is possible that this shell will be settled upon by a coral larva establishing a mutualistic relationship. This fact does not make the worm a different species. While it is true that most *A. jukesii* had anal shields with some number of cone-shaped spines, this is not universal in, or restricted to, any particular population.

The type of *A. tortus* (Selenka et al. 1883) is not with their other type specimens in the Berlin museum. They had one 25 mm worm with a longitudinal muscle layer continuous except for the anterior dorsal area where it had some separation without being clearly separate. This worm also had just one nephridium, a condition Fischer (1923) asserted was only an anomaly when he described his two worms. This has been presumed to be a separate species because it lacks unidentate hooks, now not a valid basis for separation, even if true. Their concept of spines (Stacheln) may well overlap with our idea of unidentate hooks (see their fig. 200, 201). Hérubel (1904) recorded one worm from Djibouti with no comments. When Gibbs (1978) listed this species from the Great Barrier Reef he did indicate some doubt with the (cf.) notation. Our analysis of the literature (including figures) convinces us that *A. tortus* is a junior synonym of *A. muelleri*.

When Sluiter (1902) erected *A. imbellis* he asserted that this single 13 mm worm with retracted introvert lacked hooks. Our reexamination showed this to be an error. Rings of 25–35 μm hooks exist, some with a small secondary point. The spindle muscle is attached posteriorly and it is clearly conspecific with *A. muelleri*.

Aspidosiphon inquilinis was also based on a single specimen that Sluiter (1902) differentiated from *A. muelleri* on the basis of hook and skin body morphology plus a misunderstanding of retractor origins. His specimen had lived in a scaphopod shell and the anal shield has a peculiar slant. The introvert skin is folded back over the ventral edge of the anal shield. Edmonds (1980) pointed out that Sluiter had overlooked the small cone-shaped units along the shield margin just as Edmonds' four worms exhibited. These five worms have only compressed and pyramidal unidentate hooks. They are conspecific with *A. muelleri*.

In 1912 Sluiter erected *A. exhaustus* for a single 17 mm worm taken from a scaphopod shell in the east Atlantic on the slope off Morocco. No differential diagnosis was presented and examination of the type shows it to be like the other *A. muelleri* of this region with unidentate hooks. The name went unused for 59 years, after which Murina used it four times followed by the Cutlers who used it three times for cold water worms from diverse locations. This usage was predicated on the false assumption that the real *A. muelleri* must bear some bidentate hooks.

The name *A. pygmaeus* has been used by two authors. Fischer (1921) asserted that the longitudinal muscle layer consisted of bands anastomosing so frequently that he could not count them. He did say that these were most numerous at the anterior end and ran together at the posterior end. This statement caused Stephen & Edmonds (1972) to place the species in the subgenus *A.* (*Paraspidosiphon*). When we examined the type material (four of his seven worms in good condition with introverts out and dorsal tentacles showing), we saw a continuous muscle layer with some fracturing under the anal shield, a condition common to many worms in this taxon. The coast of Chile is not a common location for *A. muelleri*, but Fischer's worms do fit this construct as do Murina's (1967a, 1971). Her second record was a repeat of the first for two worms from 150 m in the Gulf of Aden.

Aspidosiphon kovaleskii Murina, 1964, was presumed to differ from *A. muelleri* because it lacked bidentate hooks. Several populations (see Fischer 1895, Southern

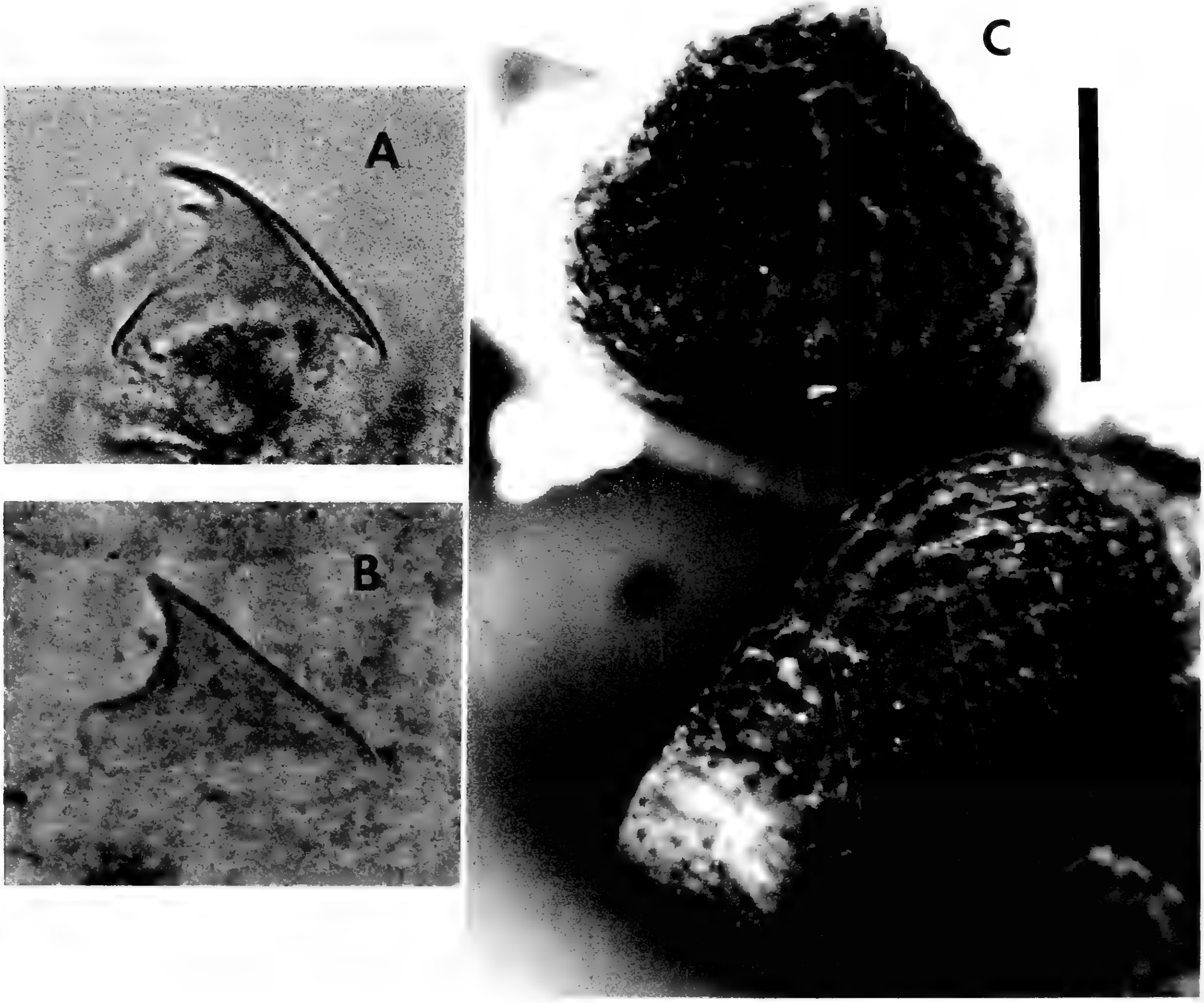

Fig. 7. *A. spiralis*: A–B, Bidentate and unidentate compressed hooks with broad bases (both 20 μm high); C, Anal shields with irregular squares in offset rows. Scale line in C = 2 mm.

1913, Gibbs 1977) of *A. muelleri* from the eastern Atlantic are reported to lack bidentate hooks. By Murina's definition these should be *A. kovaleskii.* Recently Saiz Salinas (1984:177–180) provided a detailed account of these two taxa and proposed that in both species both kinds of compressed hooks exist. He suggested that *A. kovaleskii,* if valid, might differ by having cone-shaped spines on the anal shield. He did express strong reservations about the validity of these taxa as separate and distinct biological entities; we conclude that they are not.

Aspidosiphon hispitrofus LiGreci, 1980, was based on a series of worms from Sicily. None had their introverts all the way extended, and he reported these to have no tentacles and only unidentate hooks. He did not mention the name *A. muelleri* in his paper but compared his material to *A. clavatus.* It is clear that his material is conspecific with *A. muelleri* and his unfamiliarity with the phylum led him to misinterpret the distal end of the introvert.

Distribution.—Common in the northeast Atlantic from Norway through the British Isles, the Azores and Canary Islands and West Africa (to 10°N). It extends through the Mediterranean and Red Sea into the Gulf of Aden and along the coast of east Africa to Madagascar and South Africa. The records then skip to Ceylon and sparse reports up to Japan through Thailand, Vietnam, Indonesia, and down to Australia, New Guinea, and Kermadec Island. Most of the Pacific Ocean is unpopulated by this species. One record from Juan Fernandez Island off Chile (33°S) and one from southern Brazil

(34°S) exist, but nothing else from the American hemisphere. This southern hemisphere distribution is intriguing. Throughout most of its range this species inhabits shelf depths (10–300 m), but there are several records down to 1000 m with the deepest at 2930 m.

Aspidosiphon spiralis Sluiter, 1902

Aspidosiphon spiralis Sluiter, 1902:25–26, pl. 2, figs. 9–13.—Shipley, 1903:171.—Stephen & Edmonds, 1972:236.

Material examined.—ZMUA, type specimens (V. Si. 171–174).

Discussion.—While Sluiter said this species has unidentate hooks, rings of small bidentate hooks are also present. These are about 20 μm high and the secondary point is not large (Fig. 7A, B). The unidentate hooks are about the same size and in rings. A gradual transition may exist during growth as there are some intermediate hooks. The anal shield does not have regular furrows, but neither is it made up of uniform granules. It is divided into irregular squares overlain with horny protein (Fig. 7C). The retractor muscles originate from the posterior end of the trunk. This species does not have a firm foundation (four worms), but we propose no change in its status at this time.

The three worms Shipley identified cannot be located, and we question whether he was looking at the same entity. His description of the agglutinated sand packed around the opening of the gastropod shell is much more typical of *Phascolion* species. Also, he provided no morphological information (other than color) or station data.

Distribution.—Indonesia, gastropod shells, 14–91 m.

Subgenus
Aspidosiphon (*Paraspidosiphon*)

Diagnosis.—Introvert with compressed hooks in rings, longitudinal muscle layer divided into anastomosing bands. All bore in coral or rock.

Aspidosiphon coyi
Quatrefages, 1865

Aspidosiphon coyi Quatrefages, 1865:608–609 (partim).—Baird, 1868:101.—Stephen & Edmonds, 1972:340.—Saiz Salinas, 1984:42–49.

Phascolosoma truncatum Keferstein, 1867: 50–53, pl. 6, figs. 15–18.

Aspidosiphon truncatus.—Selenka et al., 1883:118–119.—Selenka, 1885:20.—Sluiter, 1898:444; 1902:17.—Shipley, 1899b:154; 1902:132.—Hérubel, 1904: 564.—Ikeda, 1904:38–39.—Lanchester, 1905a:34.—Fischer, 1914b:15.—Benham, 1912:136.—Hammerstein, 1915: 2.—Sato, 1939:428.—Cutler & Cutler, 1979a:976.—Cutler et al., 1984:309–310.

Paraspidosiphon truncatus.—Stephen & Edmonds, 1972:258.

Material examined.—MNHN, type material (V20); *A. truncatus,* ZMUA, Sluiter's Indonesian worm (V. Si. 25.1); from Mozambique (Cutler & Cutler 1979a) and Japan (Cutler et al. 1984); USNM, unpublished material from the Gulf of Panama (21477), and Gulf of California, Puerto Penasco, Mexico (26443).

Discussion.—*A. coyi* is one of two species in this subgenus with a grooved anal shield. The primary distinction from *A. laevis* is the presence of distal rings of bidentate hooks 25–35 μm tall. However, the secondary tooth on these is very small and not consistently present. There can be unidentate compressed hooks as well as thin pyramidal hooks, and the presence of both has led to some confusion in the literature. The skin papillae towards the two ends of the trunk are large and rugose. The longitudinal muscle layer can exhibit much anastomosing and is not always clearly banded. The retractors originate from the posterior end (95–100%), the spindle muscle may bifurcate near the anus, and the wing muscle is well developed extending down to near the ventral nerve cord. The nephridia are 40–95% of the trunk length and attached for most of their length. This has not been a well defined species and the size of the data base is small. Striking similarities to *A.* (*Aspidosiphon*) *muelleri* exist (e.g., shield, retractors, hooks), and show another example of the less than clear boundary between the two subgenera.

The careful redescription of this species by Saiz Salinas (1984) brought the name *A. coyi* back from its earlier dubious status (Stephen & Edmonds 1972) and these taxa are clearly conspecific. The location of Quatrefages' specimens is not clear but is probably somewhere in the Indian Ocean.

Distribution.—Several locations in the western Indian Ocean and the western Pacific from Japan through Okinawa, Philippines, Indonesia, and Kermadec Islands. Two Latin American records of uncertain location exist: The type of *A. truncatus* from Panama (east or west coast?) and a single 3 mm worm from San Salvador (Bahamas or Galapagos?). Eastern Pacific locations for these two are supported by the USNM material from the Gulf of Panama and the Gulf of California. The former was collected in 1866 and may be part of Keferstein's type collection.

Aspidosiphon fischeri ten Broeke, 1925

Aspidosiphon fischeri ten Broeke, 1925:92–93, figs. 21–22.—Migotto & Ditadi, 1988: 250–251.

Paraspidosiphon fischeri fischeri.—Stephen & Edmonds, 1972:244–245.—Amor, 1975:118–119.—Rice, 1975:38–44.—Rice & Macintyre, 1979:311–319.

Aspidosiphon fischeri cubanus Murina, 1967b:39–42, figs. 5–7, 1967c:1331.

Paraspidosiphon fischeri cubanus.—Stephen & Edmonds, 1972:245.

Material examined.—ZMUA, type material (V. Si. 5); USNM, Venezuelan specimens identified by M. Rice (100901); unpublished specimens labeled *A. truncatus* (20726, 20725, 20727, 20836); our 1988 collections from the Caribbean.

Discussion.—The body wall of these small worms (trunks 4–16 mm) is smooth, thin, and white, but the longitudinal muscles bands cannot be easily seen through it, making it easy to misplace these worms in *A.* (*Aspidosiphon*) during preliminary sorting, i.e., they are similar to *A. A. misakiensis* or *A. A. gosnoldi.* Few, thin, ill-defined muscle bands exist that anastomose frequently and seem to fuse in the posterior part of the trunk in some worms. The long introvert (one or two times the trunk) bears rings of compressed, 18–27 μm, bidentate hooks. The proximal rings may include hooks with a very small secondary point and unidentate hooks mixed together or a few rings of just unidentate hooks. Following these are scattered, pale, pyramidal hooks 15–50 μm tall. The retractor muscles are thin and originate at or very near the posterior end of the trunk (95–100%). The nephridia are short; 33–50% of the trunk length.

When ten Broeke described this species she provided no differential diagnosis, and the differences from other species, e.g., *A. parvulus,* or those mentioned above, are not always distinct. One might make a case for this being a subspecies or an incipient or sibling species, but we propose no change now. Migotto & Ditadi (1988) question the basis for the subspecies *A. fischeri cubanus* Murina, 1967, and we agree that it only represents some of the variation within the species.

Distribution.—Numerous southern Caribbean locations from Cuba to Sao Paulo, Brazil, in shallow coral rock. Also from the Pacific coast of Panama, Ecuador, plus James and Hood Islands, Galapagos.

Aspidosiphon laevis Quatrefages, 1865

Aspidosiphon laeve Quatrefages, 1865: 609.—Baird, 1868:102.—Vaillant, 1871: 272–273; 1875: pl. 4, figs. C1–4.—DeRochebrune, 1881:233.—Saiz Salinas, 1984:55–62.

Aspidosiphon laevis.—Stephen & Edmonds, 1972:340.

Aspidosiphon cumingii Baird, 1868:102, pl.

11, fig. 2.—Selenka et al., 1883:113–115.—Fischer, 1892:85; 1922b:12.—Collin, 1892:177.—Sluiter, 1898:444; 1902:17.—Augener, 1903:321–322.—Hérubel, 1904:564.—Monro, 1931:34.—Leroy, 1936:426.—Andrew & Andrew, 1953:1.—Rice & Stephen, 1970:67.—Cutler, 1973:179–180.

Paraspidosiphon cumingii.—Stephen & Edmonds, 1972:243–244.—Edmonds, 1980:50.

Aspidosiphon major Vaillant, 1871:270–271; 1875: pl. 4, figs. A1–6.—DeRochebrune, 1881:232.

Aspidosiphon klunzingeri Selenka et al., 1883:115–116, pl. 13, figs. 187–189.—Fischer, 1896:338; 1914a:70.—Sluiter, 1898:444; 1912:20.—Shipley, 1898:471; 1899b:153.—Hérubel, 1904:564.—Monro, 1931:34.—Edmonds, 1956:308.—Wesenberg-Lund, 1957b:8–9; 1959a:196; 1959b:211–212; 1963:138.—Cutler & Cutler, 1979a:974–975; 1979b:107.

Paraspidosiphon klunzingeri.—Stephen & Edmonds, 1972:247–249.—Rice & Macintyre, 1972:42.—Rice, 1975:40–41.—Haldar, 1976:7.—Gibbs, 1978:85.

Aspidosiphon gigas Sluiter, 1884:39–57, pl. 2, figs. 1–11, pl. 2a, figs. 12–25; 1886:473; 1891:116; 1902:19.

Paraspidosiphon gigas.—Stephen & Edmonds, 1972:246.

Aspidosiphon angulatus Ikeda, 1904:45–47, figs. 11, 78–80; 1924:37.—Sato, 1939:428.—Cutler & Cutler, 1979a:974; 1981:81.—Cutler et al., 1984:308.

Paraspidosiphon angulatus.—Stephen & Edmonds, 1972:241.

Aspidosiphon speciosus Gerould, 1913:426–427, text-fig. 16, pl. 62, fig. 22.—Fischer, 1922c:13.—Migotto & Ditadi, 1988:254–257.

Paraspidosiphon speciosus.—Stephen & Edmonds, 1972:253.—Rice, 1975:38–45.—Rice & Macintyre, 1979:314.

Aspidosiphon grandis Sato, 1939:414–419, pl. 21, fig. 21, text-figs. 46–50.—Cutler & Cutler, 1981:83–84.

Paraspidosiphon grandis.—Stephen & Edmonds, 1972:246–247.

Aspidosiphon grandis obliquoscutatus Murina, 1974:1713–1715, fig. 1.

Aspidosiphon pachydermatus Wesenberg-Lund, 1937:9–16, text-figs. 4–9.

Paraspidosiphon pachydermatus.—Stephen & Edmonds, 1972:250–251.

Aspidosiphon brasiliensis Cordero & Mello-Leitao, 1952:277–282, 288–292, text-figs. 1–5.

Paraspidosiphon brasiliensis.—Stephen & Edmonds, 1972:241–243.

Aspidosiphon johnstoni Edmonds, 1980:51–53, figs. 91, 100–102.—Lopez et al., 1984:194–196.

Aspidosiphon quatrefagesi Saiz Salinas, 1984:49–55, fig. 4.

Material examined.—MNHN, type material (V20); our 1985 Hawaii and 1988 Venezuela material; *A. cumingii,* type no longer at BMNH; *A. angulatus,* Madagascar and Polynesia (Cutler & Cutler 1979a); *A. brasiliensis,* type cannot be located; *A. gigas,* ZMUA, holotype (V. Si. 8); *A. grandis,* ZITU, type specimen (24); *A. johnstoni,* two specimens from Edmonds' original material; *A. klunzingeri,* type cannot be located; ZMUA, Sluiter's Durban worm (V. Si. 9); UZMK, Wesenberg-Lund's Cape Verde material; South Africa and Cape Verde (Cutler & Cutler 1979a, b); USNM, 26437 from Saipan identified by W. K. Fisher; *A. pachydermatus,* the type cannot be located; USNM, two specimens identified by W. K. Fisher (from Saipan, 24645 and Philippines, 21480); *A. speciosus,* USNM, type material (16820, 16391, 4088); two specimens from Brazil (Migotto & Ditadi, 1988).

Nomenclatural note.—Quatrefages' original spelling is incorrect (Steyskal, pers. comm.) and when the correct ending is appended the name *A. levis* Sluiter becomes a junior homonym according to ICZN Art. 58.

Discussion.—*A. laevis* is a widespread but low density population of worms that has

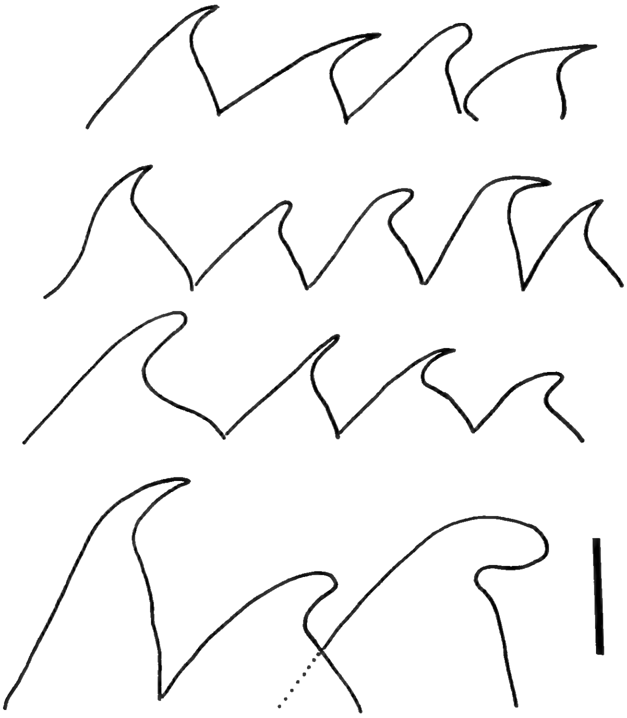

Fig. 8. Unidentate, compressed, Type A hooks of several *A. laevis* from different populations to show differences in shape and size, the latter being roughly correlated with trunk size. Scale line = 40 μm.

been given several names over the past century. One of the characters that has been weighted very differently by various authors is the nature of the caecum and its elaborations as discussed above. Setting this aside, a second issue has been the presence/absence of introvert spines. It is clear that when a few authors made reference to spines, they were either looking at scattered unidentate compressed hooks, or had a different species in hand. These worms have a solid anal shield bearing 10–15 longitudinal grooves. They have unidentate, compressed hooks, sharply pointed or blunt, in many rings (Fig. 8). These are 20–80 μm tall, hook size being roughly correlated with trunk size. Also present are a few scattered compressed hooks (referred to as spines by some earlier authors). Up to 24 tentacles surround the nuchal organ.

Internally, the pair of retractor muscles are fused for most of their length, sometimes giving the impression of a single broad muscle with the ventral nerve cord running through a notch in the base. These muscles usually have their origins from the body wall about 65–80% of the distance towards the posterior end of the trunk, i.e., well in front of the caudal shield. Another distinctive feature is the bifurcation towards the anterior end of the spindle muscle. One branch continues along the rectum into the connective tissue and wing muscle to join the body wall just anterior to the anus. The second, and often larger branch, leaves the posterior rectum going to the dorsal body wall well posterior to the anus. In many specimens the contractile vessel is not a smooth tube but has vesicular pouches or swellings along the part of its length united with the retractors (not unlike that seen in some *Golfingia* specimens, and sometimes confused with contractile vessel villi [see Cutler & Cutler 1987:750]). The rectum usually bears a caecum that may be simple or complex (see part 8, Morphological Characters section). The 25–35 longitudinal muscle bands anastomose frequently, and the circular muscle layer also subdivides into anastomosing bundles of varying degree of development. The nephridia open at, or just posterior to, the anus, are attached to the body wall for about half to two-thirds their length, and are usually more than half the trunk length.

The unpublished USNM material (21480 and 24645) consists of two worms, 44 and 123 mm long. They both have complex multiple caeca, a grooved anal shield, unidentate hooks (in the larger one these are blunt triangular and up to 60 μm tall), and in all ways match *A. laevis.*

This new arrangement reduces ten putative species to the rank of junior synonyms of *A. laevis,* a decision reached only after extended analysis. We shall not detail each case, but in a few instances there were observational errors made by the original author (for example, *A. gigas* does have rows of unidentate hooks, a spindle muscle and a complex rectal caecum, all overlooked by Sluiter). However, in most cases the different conclusions are based on judgments about within-deme variation, or simply lack of either critical comparison or differential diagnoses (e.g., Gerould [1913:427] when describing *A. speciosus* simply says: "This species resembles *A. klunzingeri* from the Red Sea" and nothing more as to how it differed). In another case Saiz Salinas (1984) erected *A. quatrefagesi* based on a suite of characters he assumed to be absent in older species while actually they were present but simply not mentioned by earlier authors.

As discussed in the Morphological Characters section, the variability in rectal appendages is great, therefore, to use such a variable character to differentiate species is unwise. A more difficult issue for us, partly because of statements by Edmonds (1980) and Rice (1975), centers on the hook morphology. We have examined many hooks from museum specimens and newly collected material, comparing hooks from small worms to those from large ones, and hooks from anterior to posterior rings in the same worm (Fig. 8). We conclude that while populations do exhibit among-deme differences, much of the alleged between species variation in shape is present within demes. Therefore, hook shape alone cannot be used to separate these putative species.

Distribution.—Widespread, but low density, in warm water Indo-West Pacific Ocean (Durban to the Red Sea, Andaman Islands, Malaya to southern Japan, Indonesia, Great Barrier Reef and several islands out to Hawaii). Also present in the Caribbean and west Atlantic (from 20°S to 31°N), then in the east Atlantic from the Canary and Cape Verde Islands to the Gulf of Guinea. Inhabits shallow water coral rock.

Aspidosiphon tenuis Sluiter, 1886

Aspidosiphon tenuis Sluiter, 1886:491–492, pl. 3, fig. 7; 1891:116; 1902:19.

Paraspidosiphon tenuis.—Stephen & Edmonds, 1972:257.

Aspidosiphon levis Sluiter, 1886:493–494, pl. 3, fig. 8; 1891:116; 1902:18.

Paraspidosiphon levis.—Stephen & Edmonds, 1972:249–250.

Aspidosiphon ambonensis Augener, 1903: 325–328, figs. 5–8.

Aspidosiphon steenstrupii var. *ambonensis* Fischer, 1922a:24–26; 1923:21.

Paraspidosiphon ambonensis.—Stephen & Edmonds, 1972:240–241.

Aspidosiphon formosanus Sato, 1939:421–424, pl. 21, fig. 23, text-figs. 55–57.—Cutler & Cutler, 1981:81–83.

Paraspidosiphon formosanus.—Edmonds, 1971:144–146; 1980:50–51.—Stephen & Edmonds, 1972:245.

Aspidosiphon havelockensis Haldar, 1978: 37–41, figs. 1–2.

Aspidosiphon speculator.—Cutler & Cutler, 1979a:975–976 (partim).

Material examined.—BMNH, (1889.6.15. 42/44) syntype; *A. levis,* ZMUA, type material (V. Si. 11); *A. ambonensis,* MNHU, type material (6956–6958); *A. formosanus,* type material cannot be located, but we have examined material from Guam and Australia identified by S. J. Edmonds; *A. speculator,* Pacific Ocean (Cutler & Cutler 1979a).

Discussion.—*A. tenuis* is here defined as having an anal shield made up of very fine dark units with a smooth overall appearance; a few very short grooves may appear around the margin. The distal rings of bidentate hooks (30–60 μm tall) lack the distinct tongue on the clear streak (Fig. 2C) and are followed by scattered, unidentate hooks (25–60 μm tall) with an internal clear streak in the distal ones. More proximally, these scattered unidentate structures have lateral reinforcing ridges. Dark pyramidal or conical hooks are absent. Internally this species is very much like *A. steenstrupii* except that only two of the ten worms dissected has a rectal caecum and the nephridia are less than 50% of the trunk length.

When Sluiter (1886) described this species he overlooked the distal rings of bidentate hooks and posterior attachment of the spindle muscle. He overemphasized the few small grooves around the margin of the anal shield. The caudal shields are not all distinctly grooved. Therefore, this is clearly conspecific with *A. levis* from the same location, and becomes the senior synonym by virtue of their position in the text.

Fischer (1922a) reduced *Aspidosiphon ambonensis* to a variety of *A. steenstrupii,* but Stephen & Edmonds (1972) elected to elevate it back to species rank since the shape of the clear area in the hook "seems to be different." We assume they based their conclusion on Augener's (1903) picture (their fig. 29K is Augener's fig. 6). Our examination of the type material (19 worms) confirms Augener's perceptions and supports our position that this population is conspecific with *A. tenuis,* but different than *A. steenstrupii* in accordance with Stephen & Edmonds (1972).

Sato (1939) erected *A. formosanus,* but Cutler & Cutler (1981) reduced it to a junior synonym of *A. steenstrupii.* Given our current understanding we would move *A. formosanus* into the synonomy of *A. tenuis* as it shares its attributes.

In 1978 Haldar described *Aspidosiphon havelockensis.* In his unpublished dissertation (pers. comm.) it is reduced to a junior synonym of *A. steenstrupii ambonensis* differentiated from the nominate form on the basis of hook, spine, and papillae structure. We agree with his conclusions as far as they go. However, we now consider both these names to be junior synonyms of *A. tenuis.*

Upon reexamination, the specimens Cutler & Cutler (1979a) identified as *A. speculator* from the Solomon Islands and Thailand belong in this taxon.

Distribution.—Andaman Islands to Thailand, Formosa, and Guam, out to the eastern Caroline Islands and down through the Solomon Islands to the Great Barrier Reef and Indonesia.

Aspidosiphon parvulus Gerould, 1913

Aspidosiphon parvulus Gerould, 1913:425–426, pl. 61, fig. 17, text-fig. 15.—Stephen & Edmonds, 1972:233–234.—Cutler, 1973:178–179.

Aspidosiphon spinoso-scutatus Fischer, 1922c:13–14, text-figs. 2–3.—Murina, 1967b:42; 1967c:1332.

Paraspidosiphon spinososcutatus.—Stephen & Edmonds, 1972:254.—Rice, 1975:38–45.

Material examined.—USNM, type (15118); western north Atlantic (Cutler 1973); our 1988 Venezuelan worms; *A. spinoso-scutatus,* MNHU, type (6053).

Discussion.—This species shares many attributes with *A. fischeri,* but the shield morphology seems consistent and distinctive. Centrally it is made up of larger flat plates; these are sometimes arranged in rows giving an impression of ridges and grooves. Ventrally and laterally the units become smaller, scattered, wart- or cone-shaped. The shields have a diffuse boundary where the units grade into coarse trunk papillae. At both ends of the trunk these darker papillae are located in rectangles that remind one of *Sipunculus* skin. The hooks (bidentate and unidentate in rings, scattered unidentate, and pyramidal, Fig. 1E) are 25–35 μm tall. The 10–12 short tentacles may appear webbed together with connective tissue, and there are about 24 anastomosing longitudinal muscle bands. These bundles are generally quite distinct in worms over 5 mm long, more so towards the anterior end (see Cutler 1973:178 where Gerould's 3 and 4 mm specimens are discussed). The nephridia are 50–75% of the trunk length.

Distribution.—Western Atlantic Ocean from Cape Hatteras through the Caribbean to Venezuela; often found together with *Themiste alutacea* and *Nephasoma pellucidum* in branching corals.

Aspidosiphon planoscutatus
Murina, 1968

Aspidosiphon planoscutatus Murina, 1968:1722–1724, figs. 1–2; 1971:78.

Material examined.—ZIAS, type material.

Discussion.—This taxon is based on two specimens and is very similar to *A. steenstrupii* but has only unidentate compressed hooks on the introvert. Also, the shield units are smaller (fine grained like *A. zinni*) and the trunk is densely covered with more obvious skin bodies. The nephridia are 85% of the trunk length.

The Red Sea is a marine habitat with unusual abiotic conditions (e.g., high salinity, low oxygen, high temperature) that may restrict gene flow and favor selection of different allelic frequencies. The absence of bidentate hooks on the introvert may be a real difference, but we cannot verify this. Despite our reservations we are leaving the name because of the habitat. It is hoped that more collecting in the area will produce additional material for analysis.

Distribution.—Red Sea at 40 m.

Aspidosiphon steenstrupii
Diesing, 1859

Aspidosiphon steenstrupii Diesing, 1859:767, pl. 2, figs. 1–6.—Quatrefages, 1865:610.—Selenka et al., 1883:116–118.—Sluiter, 1886:489–490; 1891:115; 1902:18.—Whitelegge, 1899:394.—Shipley, 1899b: 153–154; 1902:131–132; 1903:171.—Ikeda, 1904:40–41; 1924:38.—Hérubel, 1904:564.—Lanchester, 1905b:39.—Fischer, 1914a:70–71; 1914b:13; 1922a: 23; 1922c:13; 1923:21; 1926:108; 1931: 139.—ten Broeke, 1925:93–94.—Monro, 1931:34.—Sato, 1935:315–316; 1939: 424–426.—Leroy, 1936:426; 1942:36–38.—Stephen, 1942:253.—Stephen & Robertson, 1952:441.—Edmonds, 1956: 307–308.—Wesenberg-Lund, 1959a:197–198; 1963:138.—Murina, 1967b:42; 1981:12–13.—Cutler, 1977a:148.—Cutler & Cutler, 1979a:976; 1979b:107–108.—Cutler et al., 1984:308–309.—Migotto & Ditadi, 1988:259–260.

Paraspidosiphon steenstrupii steenstrupii.—Stephen & Edmonds, 1972:254–255.—Rice, 1975:38–45.—Haldar, 1976:8.—Rice & Macintyre, 1972:42; 1979:311–319.—Edmonds, 1980:51.

Aspidosiphon steenstrupii var. *faciatus* Augener, 1903:322–325, figs. 1–4.

Paraspidosiphon steenstrupii fasciatus.—Stephen & Edmonds, 1972:255–256.

Aspidosiphon fuscus Sluiter, 1881:86–108; 1886:474; 1891:116; 1902:19.—Selenka et al., 1883:116.

Aspidosiphon semperi ten Broeke, 1925:92, text-figs. 18–20.—Gibbs & Cutler, 1987: 56.

Paraspidosiphon semperi.—Stephen & Edmonds, 1972:252.

Aspidosiphon speculator Selenka, 1885:19–20, pl. 4, figs. 24–27.—Fischer, 1914b:71; 1920:413.—Wesenberg-Lund, 1959b: 213.—Cutler & Cutler, 1979a:975–976 (partim).—Not Saiz Salinas, 1986a:11–14.

Paraspidosiphon speculator.—Stephen & Edmonds, 1972:253–254.

Aspidosiphon makoensis Sato, 1939:419–421, pl. 21, fig. 22, text-figs. 51–54.—Cutler & Cutler, 1981:82–83.

Paraspidosiphon makoensis.—Stephen & Edmonds, 1972:250.

Aspidosiphon trinidensis Cordero & Mello-Leitao, 1952:283–286, 292–294, figs. 6–10.—Cutler & Cutler, 1979b:108; 1980c: 206.

Paraspidosiphon trinidensis.—Stephen & Edmonds, 1972:257–258.

Aspidosiphon exostomum Johnson, 1964: 331–332, pl. 7.

Paraspidosiphon exostomus.—Stephen & Edmonds, 1972:244.

Aspidosiphon ochrus Cutler & Cutler, 1979a: 976–979, figs. 15–17.—Edmonds, 1987: 204.

Material examined.—ZMUA, Sluiter's 1902 specimens (V. Si. 21); our Pacific and Caribbean material; Brazil (Migotto & Ditadi 1988); *A. semperi,* ZMUA, types (V. Si. 14); *A. exostomum,* RSME, type (1965.32.2); *A. speculator,* BMNH, 1885. 12.3.28, syntype; specimens from Canary Islands and Spain identified by J. Saiz Salinas; Madagascar (Cutler & Cutler 1979a).

Discussion.—We came to the present understanding of *A. steenstrupii* only after looking at many worms from diverse locations, and carefully reexamining the literature. The color of the anal shield was a confusing element. It now seems clear that a range of colors is possible, from almost white to very dark brown, and that additional calcareous material may be deposited externally, thus masking the underlying units. Geographic variation seems present with the Atlantic Ocean populations being dark, the mid Pacific Ocean populations being pale and the Indian Ocean populations exhibiting a mixture (a higher frequency of dark shields in populations near continents, rare in island populations).

The other major issue centers around the hooks. We are defining this species as having bidentate hooks in rings (30–60 μm tall; up to 90 μm in worms over 25 mm long), most with a tongue-like extension on the internal clear streak (Fig. 2B), and no unidentate compressed hooks. The proximal introvert does bear many scattered, dark, pyramidal hooks about 30–60 μm tall.

Internally the pair of retractor muscles originate about 70–85% of the distance to the posterior end of the trunk, not correlated with trunk size (see Table 2). The nephridia are commonly 50–80% of the trunk length and attached to the body wall for 50–75% of their length (over 90% in three worms). A simple rectal caecum was observed in 21 of the 30 worms dissected. The longitudinal muscle bands anastomose (14–22 anteriorly and 20–28 posteriorly), and the number is not correlated with trunk length.

J. Silverstein (pers. comm.) determined the karyotype on a Japanese population. The 2N number is 20 with five pairs of meta/submetacentric and five pairs of telo/subtelocentric chromosomes.

When Selenka (1885) erected *A. speculator* he made no reference to any other species (no differential diagnosis or key). In Stephen & Edmonds (1972) the key separates these two species based on the location of the retractor origins that were imprecisely stated in the original. In the syntype, the origins are at 75% of the distance to the posterior end of the trunk, well within the *A. steenstrupii* range. The internal structure of the compressed hooks and the nature of the pyramidal hooks, shield, and other characters all match this species. The part of Cutler & Cutler (1979a) collection that belongs here are the Madagascar worms, the remainder are *A. tenuis.* Saiz Salinas (1986a) used *A. speculator* for a collection that we consider to be *A. misakiensis.*

Fischer (1922a) reduced Augener's 1903 *A. steenstrupii fasciatus* to a junior synonym of the nominate form where it remained until Stephen & Edmonds (1972) resurrected its subspecies rank. They based their decision on the clear area in the hook and color differences on the shield and mid-trunk. Our examination of the type, within the context of this study, convinces us that Fischer's action was correct.

When ten Broeke (1925) described *A. semperi* from Curacao she asserted that it had four retractor muscles, but Gibbs & Cutler (1987:56) determined that there are only two. Despite the pale colored anal shield *A. semperi* is clearly conspecific with *A. steenstrupii,* a conclusion confirmed by our recent collections in Curacao.

Sato's two species, *Aspidosiphon formosanus* and *A. makoensis* were reduced to the status of junior synonym in Cutler & Cutler (1981). We reaffirm that action for the latter but not the former (see below).

Aspidosiphon trinidensis was described from a single worm that cannot be located. The two subsequent reports were also based on single worms (in Cutler & Cutler 1980c, it should have read 25 mm trunk, not 125 mm). Reexamination of the two available worms revealed a few distal rings of bidentate hooks that had been overlooked. Those structures reported as unidentate hooks are now interpreted as pyramidal hooks. Cordero & Mello-Leitao's worm (1952) had its introvert entirely withdrawn and the objects they described as unidentate hooks were not in rings. From their words and drawings we interpret these as pyramidal hooks. With this understanding (and the assumption that they too overlooked the bidentate hooks) nothing separates *A. trinidensis* from *A. steenstrupii,* thus we place it in synonomy.

Aspidosiphon exostomus (Johnson 1964) was alleged to be different because of the dorsal crown of tentacles. This was clearly visible as the esophagus was protruding through the mouth. However, we now know that all members of the Aspidosiphonidae have dorsal tentacles and this taxon is clearly not unique.

When Cutler & Cutler (1979a) described *A. ochrus* we were working within a different experiential framework. As a result of the present analysis, it clearly should be reduced to a junior synonym. In that same paper we identified a specimen from Madagascar as *A. speculator* that, upon reexamination, we now consider to be an *A. steenstrupii.* Edmonds (1987) used the name *A. ochrus* after consulting with us, but these also are *A. steenstrupii* with pale anal shields.

Distribution.—Throughout the western and northern Indian Ocean, Queensland through Indonesia and the South China Sea to southern Japan, out through the western Pacific islands to Hawaii. Also collected from numerous Caribbean locations, in the eastern Atlantic only from the Cape Verde Islands and the Gulf of Guinea. It lives in shallow water coral rocks.

Zoogeographical Summary

Ten of the 19 species live in the tropical/subtropical western Atlantic Ocean and Caribbean Sea, an area bounded by Cape Hatteras on the north and the Amazon delta on the south (*A. albus, A. exiguus, A. gosnoldi, A. parvulus, A. fischeri, A. mexicanus, A. elegans, A. laevis, A. steenstrupii,* and *A. misakiensis).* The first four of these are endemic to the region. The fifth extends into the eastern Pacific (Panama to Galapagos). The sixth extends its range in the other direction, to the eastern Atlantic (between Iberia and the Gulf of Guinea) but nowhere else. The next three species are circum-tropical while the last is found on both sides of the Atlantic Ocean and off Japan and Australia.

Two species are found in the eastern Atlantic and elsewhere that do not live in the western part (*A. venabulus* from both sides of Africa, and *A. muelleri,* see below). Also in the north Atlantic (plus one record from the Mozambique Channel) is *A. zinni,* the one bathyal/abyssal member of this genus.

Of special note is *A. muelleri,* since it has the most widespread distribution, almost cosmoplitan in temperate waters. Two apparent gaps occur; in the western Atlantic (except for one record off southern Brazil), and in the eastern Pacific there is only one record off Chile. This is the most eurytopic *Aspidosiphon* living in a much wider variety of temperatures and depths than other species.

Six species are widely distributed within the Indo-West Pacific area. *Aspidosiphon gracilis schnehageni* and *A. coyi* extend into the eastern Pacific Ocean. Three are also found in the Caribbean (as above). The remaining two do not get to Hawaii or the Atlantic (*A. gracilis gracilis* and *A. tenuis*). Two species (*A. thomassini* and *A. spiralis*) are more restricted within the Indian Ocean and *A. planoscutatus* is known only from a single collection in the Red Sea.

Of particular interest is the number of endemic species in the warm water Atlantic/eastern Pacific Ocean (six) when compared to the Indo-West Pacific area (five). Of the 19 species, 13 live somewhere in the Atlantic Ocean while 11 occupy some part of the Indo-West Pacific (six of these are in both areas). These data have interesting evolutionary implications suggesting that the traditional "center of origin" hypothesis for marine invertebrates (Indo-West Pacific) may not fit *Aspidosiphon.*

While it is true that common, widespread species bore in coral or soft rock, 11 species (58%) do not occupy this stereotypical aspidosiphonid niche, i.e., they live in discarded mollusc shells (8), arenaceous foraminiferan tests (1), or interstitially (2).

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AXIOTHELLA CROZETENSIS, A NEW SPECIES OF MALDANID POLYCHAETE FROM CROZET ISLANDS (INDIAN OCEAN)

Patrick Gillet

Abstract.—A new species of Annelida Polychaeta, *Axiothella crozetensis,* is described from Crozet Islands (46°46.6′S and 50°28.4′E, Indian Ocean). Specimens were collected from depths of 1350 to 1440 m during the MD.08/Benthos Expedition (7 Mar 1976–26 Apr 1976). *Axiothella crozetensis* is compared with all described species of the genus *Axiothella.*

Maldanid polychaetes, called bambooworms, are capitelliform, usually long and truncate; the prostomium with nucal organs and a cephalic keel, without appendages, is fused to the buccal segment. Reviews of the family are found in Arwidsson (1907). *Axiothella crozetensis* is the first species of the genus *Axiothella* collected at a great depth. Holotype and paratypes are deposited in the Institute of Fundamental and Applied Research Museum (I.R.F.A.-MAL-047).

Genus *Axiothella* Verrill, 1900

Type species.—*Axiothella catenata* (Malmgren, 1865:190–191).

Diagnosis.—Eighteen to 20 setigers present. Rostrate uncini present in all neurosetigerous segments including the first three neuropodia. Each uncinus with lateral series of teeth above main fang without barbules. Acicula absent. Rim of cephalic plate entire or incised. Anal plaque funnel-shaped; anal cirri of different lengths or as crenulations. Mangum (1962) reviewed the status of the genus *Axiothella* which she placed as a subgenus of *Clymenella* Verrill (Mangum 1962, 1966). This decision did not gain acceptance and authors now recognize the original generic status.

Axiothella crozetensis, new species
Figs. 1–2

Material examined.—Holotype Crozet Islands (19 Apr 1976), Station 70: Sampling DC 280, 46°46.6′S and 50°28.4′E; Paratypes (2) Crozet Islands (19 Apr 1976), Station 70: DC 280, 46°46.6′S, 50°28.4′E. Materials deposited to I.R.F.A. Museum IRFA MAL 047.

Description.—Holotype has 18 setigers and two achaetous preanal segments. Body without color pattern in alcohol. Prostomium longer than wide (1.4 mm long; 0.70 to 0.90 mm wide) with the cephalic plate 0.60 mm long (Fig. 1F). First setiger 1.4 mm long, second setiger 2 mm long, diameter ranging from 0.50 to 0.75 mm. Prostomium well developed with entire rim, not incised. Nucal organs long and parallel; ocelli absent. Buccal segment as long as the first setiger (Figs. 1A, 2A). First setiger depressed anteriorly near fascicle of capillary setae. Notosetae numbering about 15 per fascicle, short and long, are all capillary smooth (Fig.

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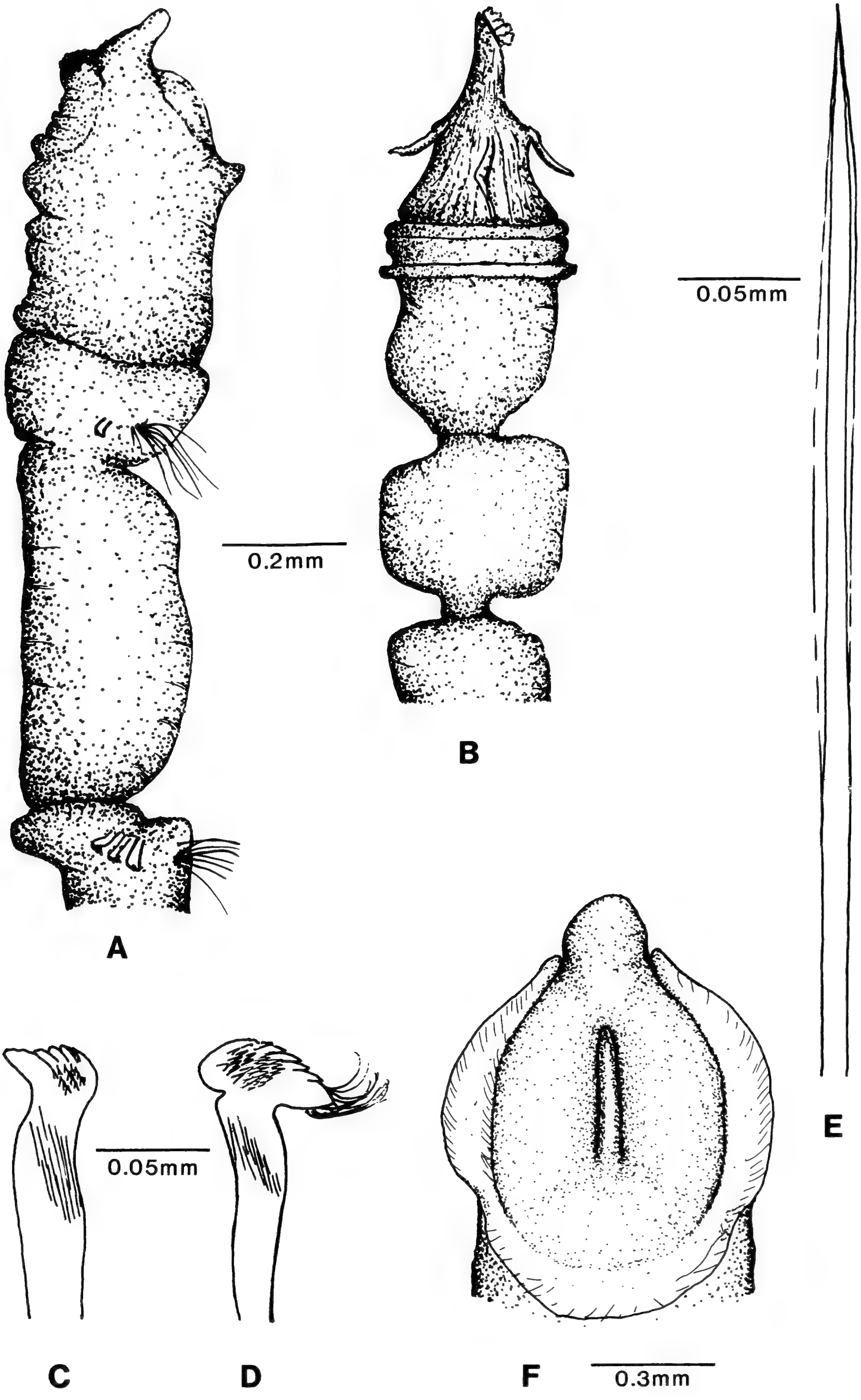
Fig. 1. *Axiothella crozetensis*: A, Anterior region lateral view; B, Posterior region; C, Uncinus from setiger 2; D, Uncinus from setiger 4; E, Capillary setae from setiger 4; F, Cephalic plate frontal view.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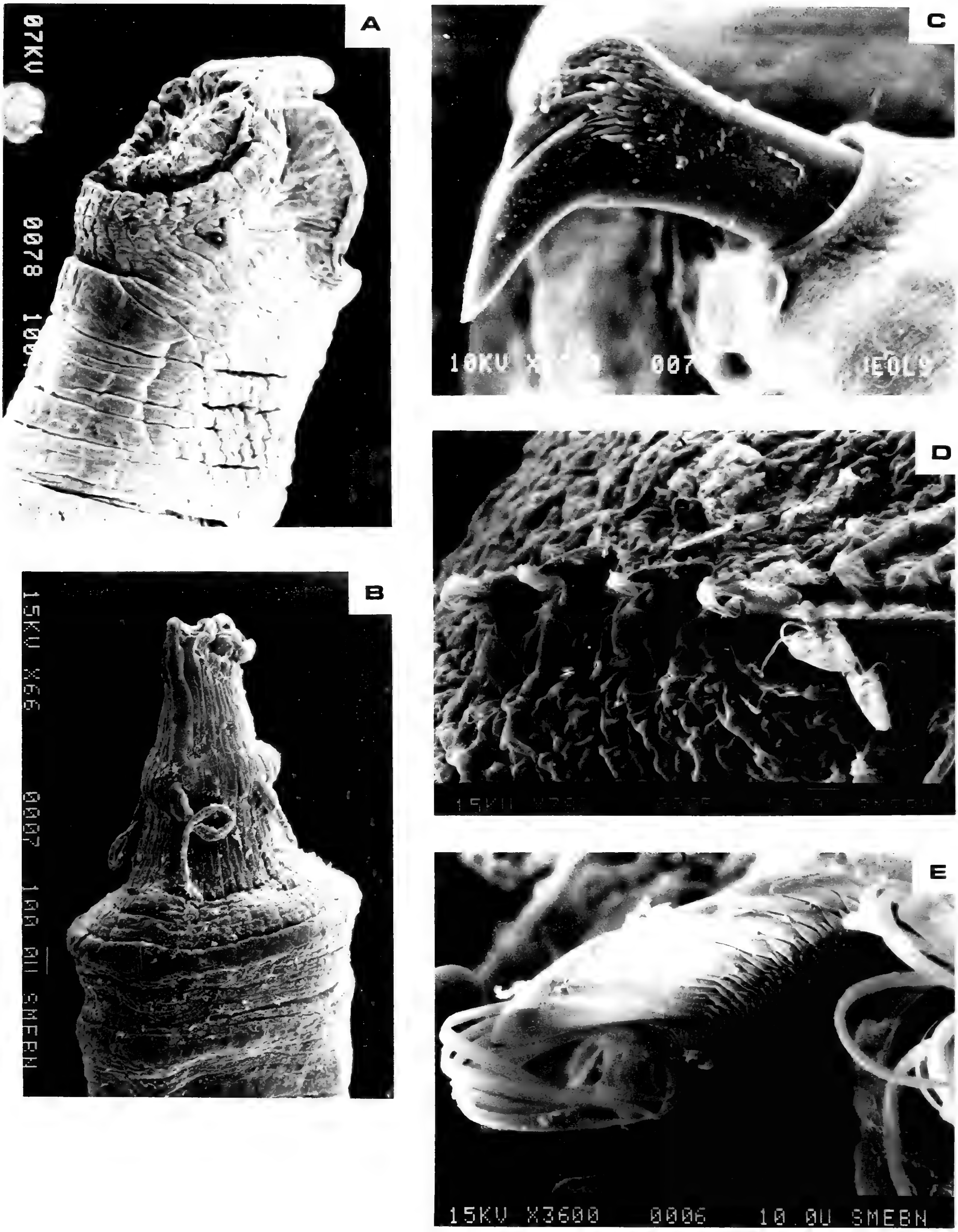

Fig. 2. Scanning electron micrographs of *Axiothella crozetensis*: A, Anterior region lateral view; B, Posterior region; C, Uncinus from setiger 3; D, Row of uncini from setiger 4; E, Uncinus from setiger 4.

1E). Spinulose, barbelate and bipennate notosetae are absent. Neurosetae of the first setiger are 1–2 uncini per side, each with 4–6 apical teeth without barbules (Figs. 1C, 2C). The second setiger has two or three uncini, the third setiger has three uncini and the fourth setiger six uncini. Uncini from setiger 4 to the end of the worm have barbules below the main fang and one row of six or seven vertical teeth and many smaller ones on each side (Figs. 1D, 2D, 2E). Glandular area absent. The posterior region has two achaetous preanal segments. Pygidium is prolonged posteriorly as a cone with three long anal cirri, each of equal length and nearly the same as the length of the pygidium (Figs. 1B, 2B). The anus is subdorsal with a ventral value.

Discussion.—*Axiothella crozetensis* belongs to the subfamily Euclymeninae, genus *Axiothella* Verrill, 1900, because of the presence of rostrate uncini on the first three neuropodia. Other genera without acicular spines are *Gravierella* Fauvel, 1919 and *Macroclymenella* Augener, 1926, but the number of segments in these genera is more than 30. Species of the genus *Maldanella* McIntosh, 1885 have the first setiger with notosetae only, and those of the genus *Clymenura* Verrill, 1900 have a flanged collar on setiger 4 and a large triangular glandular field on setiger 8.

Axiothella crozetensis differs from other species of *Axiothella* in that it has only one to three uncini on the first three setigers and a prolonged anal cone with three long anal cirri as in the genus *Clymenura* (Table 1). Among the species living in the Antarctic and Subantarctic regions *Axiothella jarli* Kirkegaard, 1959 (Angola, Cape) differs in having from three to seven hooks on the first three setigers. The structure of the pygidium is different with 18 anal cirri alternately long and short. *Axiothella antarctica* Monro, 1930 differs in having three uncini on the first setiger and numerous on the second and third setigers, pygidium with a long single anal cirrus and fifteen shorter cirri. *Axiothella quadrimaculata* Augener, 1914 has numerous uncini on the first three setigers, only one achaetous preanal segment and also differs in lacking anal cirri. Hartmann-Schröder & Hartmann (1984) found two different species of *Axiothella* sp. at Murat Bay, Australia: *Axiothella* sp. A has uncini with five teeth and short barbules and *Axiothella* sp. B has six teeth and long barbules. This species was also found at Blanche Harbour, Australia (Hartmann-Schröder 1985).

Axiothella crozetensis has been found at depths exceeding most records given for other species of *Axiothella* living in the intertidal zone except *Axiothella constricta* Claparède, 1868 at 35–750 m (Tarente) and *Axiothella catenata* Malmgren, 1865 at 10–900 m (Arctic) (Table 1). *Axiothella quadrimaculata* lives in southwest Australia at 3 to 12.5 m on rocks or sand (Augener 1914), at Kerguelen Islands at 20–50 m (Monro 1939), in South Africa at 0–54 m (Day 1961) and at Marion and Prince Edward islands on the shore with ascidians and amphipods (Day 1971). *Axiothella crozetensis* was dredged from 1350 to 1440 m in mud flats with associated fauna of Annelida Polychaeta including *Nephtys hombergii, Trypanosyllis gigantea, Ampharete kerguelensis* and *Melinna cristata.* Morphologically and ecologically these two species differ accordingly: *Axiothella quadrimaculata* lives on rocky bottoms near the shore from 0 to 54 m and *Axiothella crozetensis* lives in mud flats at a depth of about 1400 m. These two species differ from others species of *Axiothella* by the structure of the pygidium. Based on this character, the genus *Axiothella* is in need of revision. *Axiothella catalinia* (Hartman 1969) was transferred to *Maldanella* by Kudenov and Read (1978) because of the absence of uncini on the first setiger, and *Clymenura brasiliensis* (Mangum 1966) must be referred to *Axiothella.*

Habitat.—Subantarctic, Crozet Islands

Table 1.—Species of the genus *Axiothella* Verrill, 1900 (N: numerous uncini).

Species	Distribution, depth (m)	Number of setae setigers 1 – 2 – 3	Achaetous segments	Pygidial cirri
A. antarctica Monro, 1930	Antarctica, 200–344	3 – N – N	5	1 long cirrus, 15 short cirri
A. australis Augener, 1914	Australia, India, 3–12.5	N – N – N	2	7–11 long, 23–30 short cirri
A. brasiliensis Mangum, 1966	Brazil, 1–12	4/6 – 4/6 – 3/5	2	alternately short and long
A. catenata Malmgren, 1865	Arctic, 10–900	8 – 9 – 15	4	22 alternately short and long
A. cirrifera Langerhans, 1880	Madeira, ?	1 to 6	2	1 median cirrus, 14 papillae
A. constricta Claparède, 1868	Italy, 35 to 750 m	N – N – N	3	1 long cirrus, numerous short
A. jarli Kirkegaard, 1959	Angola, Cape, 35–100	3 – 6 – 7	2	18 alternately short and long
A. mucosa Andrews, 1891	United States, Intertidal	12 – N – N	3/4	20 to 30 short and long
A. obockensis Gravier, 1905	Red Sea, India, Intertidal	N – N – N	2	1 long cirrus numerous short
A. quadrimaculata Augener, 1914	Subantarctic, 11–50	N – N – N	0/1	without cirri
A. rubrocincta Johnson, 1901	United States, Intertidal	N – N – N	2/3	1 long cirrus, 18/30 short/long
A. serrata Kudenov and Read, 1978	New Zealand, Intertidal	6 – 7 –10	0	1 long cirrus, 21 to 42 cirri
A. somersi Verrill, 1900	Bermudas, Intertidal	3/4 – 4/5 – 6/8	2	24 alternately short and long
A. tambalagamensis Pillai, 1961	Ceylon, ?	N – N – N	0	numerous cirri, 13 papillae
A. zetlandica McIntosh, 1915	North Sea, 110–183	2/3 – 4 – 4	?	44 alternately short and long
A. crozetensis, present work	Crozet Island, 1350–1440	1/2 – 2/3 – 3	2	3 long cirri
A. sp. Wesenberg-Lund, 1949	Iranian Gulf, 71	25 – 25 – 25 no accessory teeth	?	?
A. sp. Imajima, 1963	Kamchatka, 68	10 – N – N	?	?
A. sp. Wolf, 1984	Gulf of Mexico, 19–43	2/3 with barbules	1	1 long cirrus, 20–24 short
A. sp. Hartmann-Schröder and Hartmann, 1984	Australia, ?	1 to 4	2	1 long cirrus, 15 short cirri

(South of Penguins Island) from 1350 to 1440 m in mud flats.

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PARAPROCERASTEA CROCANTINAE, A NEW GENUS AND SPECIES (POLYCHAETA: SYLLIDAE: AUTOLYTINAE) FROM THE SPANISH MEDITERRANEAN

Guillermo San Martín and Carmen Alós

Abstract.—*Paraprocerastea crocantinae,* a new genus and species of Autolytinae (Syllidae: Polychaeta) from off Cabo de Creus and Cabo de Gata both on the Mediterranean coasts of Spain, is described. The new genus is discussed and compared with the remaining genera of Autolytinae. Finally, a key to the genera of Autolytinae is given.

In a study of Alós (1988) on the polychaetous annelids from the Cabo de Creus coast (Spain), two specimens of a syllid were found. These specimens were originally identified as an unknown species of *Procerastea* Langerhans, 1884. Another specimen, longer than the others, was collected by the first author in a study of the polychaetes from *Posidonia oceanica* beds along the southern coast of Spain. This latter study was part of a project on the invertebrates from this habitat in Southeast Spain.

A new detailed study of all these specimens reveals the presence of small dorsal cirri on all segments. This character definitively separates these specimens from the genus *Procerastea* which only has dorsal cirri on the first setiger. This new genus is named *Paraprocerastea* and is overall very similar to *Procerastea.*

Two other genera of Autolytinae seem also to be related to *Paraprocerastea*: *Alluaudella* Gravier, 1905, from Madagascar and the Arabian Gulf, and *Phyllosyllis* Ehlers, 1897, from Antarctica. *Paraprocerastea* differs from both genera by having a pharynx with a trepan. It differs further from *Phyllosyllis* by having a different disposition of anterior segments and different setae, and from *Alluaudella* by having antennae and dorsal cirri of a different shape.

Observations and measurements were made by means of a microscope with interference contrast optics. Drawings were made by means of a drawing tube. Length measurements exclude antennae and anal cirri; width measurements were taken at proventricular level, excluding dorsal cirri and setae. The holotype and paratype from off Cabo de Creus are preserved in 70% ethanol. The other paratype is in a permanent microscopical preparation made with glycerin jelly. All type material is deposited in the Museo Nacional de Ciencias Naturales de Madrid (MNCNM), Spain.

Family Syllidae Grube, 1850
Subfamily Autolytinae Rioja, 1925
Paraprocerastea, new genus

Diagnosis.—Body small, short, without segmentarial ciliation, small number of setigers. Prostomium relatively large, partially covered by an occipital flap from tentacular segment. Four dorsal eyes and two ventral eyespots; three thick, club-shaped antennae. Palps reduced, completely fused. Two pairs of tentacular cirri. Tentacular cirri and dorsal cirri of first setiger club-shaped. Remaining dorsal cirri minute, egg-shaped. Two subrectangular, relatively long, anal cirri. Simple setae of only two kinds: bayonet-shaped setae and falcate setae. Pharynx slender, with a distal trepan.

Remarks.—Gidholm (1967:177) classified the genera of Autolytinae in two natural groups. One group, composed of *Proceraea* Ehlers, 1864, *Procerastea* Langerhans, 1884, and *Virchowia* Langerhans, 1879 (=*Umbellysyllis* Sars, 1869; according to Hartman 1959), is characterized by having internal parapodial glands, segmental ciliation reduced or absent, bayonet setae of the thick type, and stolonization by anterior scissiparity. The other group, composed of *Autolytus* Grube, 1850, and *Myrianida* Milne Edwards, 1845, is characterized by external parapodial glands, well developed segmentarial ciliation, bayonet setae of the slender type, and stolonization, if present, of a type other than anterior scissiparity. Gidholm did not include two, poorly known, genera of this subfamily, *Phyllosyllis* Ehlers, 1897 and *Alluaudella* Gravier, 1905. These two genera have unarmed pharynges, lack segmental ciliation, and apparently lack bayonet-shaped setae. The parapodial glands have not been described; they could constitute a third natural group.

Another genus, *Odontoautolytus* Hartmann-Schröder, 1979, has an uncertain position between the subfamilies Eusyllinae and Autolytinae, because it is very similar to *Odontosyllis* Claparède, 1863, but lacks ventral cirri.

Imajima & Hartman (1964) described another genus, *Autosyllis,* on the basis of a solitary Polybostrichus stolon. Consequently, it is very difficult to know the characters of the atokous form and determine to which group it belongs. According to Gidholm, the specimen of *Autosyllis* is very similar to a male Polybostrichus of *Umbellysyllis.*

Paraprocerastea differs from *Procerastea* in having minute dorsal cirri on all segments, whereas *Procerastea* has dorsal cirri only on setiger 1. However, the stolons of *Procerastea* have dorsal cirri on all setigers (Fauvel 1923:326, Allen 1921:135–137) similar to those of *Paraprocerastea,* and the segments in regeneration of adults have very small dorsal cirri (see Allen 1921:135, 140). These observations indicate a very close relationship between both genera. Another difference is the peculiar, slender, bayonet setae of *Paraprocerastea,* whereas the bayonet setae of *Procerastea* are thicker, with several short spines and a long filament, very similar to those of *Proceraea* (see Gidholm 1967: 207). On the other hand, the setae of *Paraprocerastea crocantinae* are very similar to the simple setae of *Procerastea halleziana* Malaquin, 1893 (see Malaquin 1893:81, Fauvel 1923:326, Gidholm 1967:207, Alós 1988:244), *P. nematodes* Langerhans, 1884 (see Langerhans 1884:249, Fauvel 1923:326, Gidholm 1967:207) and *P. australensis* Hartmann-Schröder, 1987 (see Hartmann-Schröder 1987:65). These simple setae probably originated by shaft and blade fusion of compound setae; however, no compound setae or slightly fused setae have been found on *Paraprocerastea crocantinae.* Finally, *Procerastea* has nuchal epaulettes and *Paraprocerastea* has an occipital flap.

The genus *Phyllosyllis* is also very similar to *Paraprocerastea* in having cylindrical to club-shaped anterior appendages, similar in length to body width, and very small, pyriform to egg-shaped dorsal cirri on the remaining segments. However, *Phyllosyllis* has an unarmed pharynx, only compound setae and setae on the tentacular segment (Hartman 1964:83); this last character is unusual in the family Syllidae and, in our opinion, another interpretation is possible; according to the drawings of Ehlers (1897) and Hartman (1964), *P. albida* has only a pair of short tentacular cirri on a reduced tentacular segment, and the longer cirri are actually the dorsal cirri of the second segment (first setiger).

Finally, *Alluaudella* is also very close to *Paraprocerastea* but has shorter antennae, an unarmed pharynx, well developed dorsal cirri similar throughout the body, whereas the latter genus has long antennae, a pharynx with a trepan, and short, egg-shaped, dorsal cirri from the second setiger. On the other hand, *P. crocantinae* is similar to *A.*

madagascarensis in having an occipital flap and in the shape of the setae.

Type species.—*Paraprocerastea crocantinae.*

Etymology.—The generic name is referred to the close relation with the genus *Procerastea*; gender is feminine.

Paraprocerastea crocantinae, new species

Fig. 1

Material examined.—Cala Taballera, off Cabo de Creus, Gerona, Spain; calcareous concretions of *Mesophyllum lichenoides* and *Lithophyllum expansum*; 12 m depth; holotype, complete, but left dorsal cirri of first setiger lacking. Isle Massa d'or, off Cabo de Creus; calcareous concretions of *Lithophyllum expansum*; 20 m depth; one paratype, complete, but median antenna lacking. Off Los Genoveses Inlet, Almería, Spain; rhizomes of *Posidonia oceanica*; 3 m depth; one paratype, complete, but antennae lacking.

Etymology.—The name of the species is dedicated to the research vessel *Crocantina* of the Departamento de Biología (Zoología), Universidad Autónoma de Madrid.

Description.—Body relatively short and thick, cylindrical, 3.4 mm length, 0.32 mm width, 33 setigers, without color marking, without segmentarial ciliation. Prostomium (Fig. 1A, B) proportionally large, circular; four large eyes in rectangular arrangement and two small ventral eyespots. Palps very reduced, practically nonexistent, completely fused to one another. Three thick antennae, cylindrical to club-shaped, lateral antenna more than twice prostomium length, originating on anterior margin of prostomium; median antenna approximately three times longer than lateral antennae, originating between anterior eyes (Fig. 1A). Tentacular segment ventrally reduced, dorsally prolonged in an occipital flap, covering posterior half of prostomium; two pairs of tentacular cirri, similar in shape to antennae, dorsal ones approximately half of lateral antennae length, ventral ones somewhat shorter (Fig. 1A, B). Dorsal cirri of first setiger club-shaped, similar in length to dorsal tentacular cirri; dorsal cirri of remaining segments minute, egg-shaped to oval (Fig. 1A, B). Parapodia short, conical, without ventral cirri (Fig. 1E). Setae simple and of only two kinds: bayonet-shaped setae and falcate setae; similar on all segments, without dorsoventral gradation in shape (Fig. 1E); parapodia each with one dorsal bayonet-shaped seta of a peculiar kind, relatively thin, ending in four short spines and a long filiform filament (Fig. 1F, J), and from three to five thick simple falcate setae, bifid, with two acute, curved, unequal teeth, provided with a subterminal thickened crown of a complete ring of small spines (Fig. 1G, H, K, L). Aciculae numbering 1–2 per parapodium, thin, with rounded tip (Fig. 1I). Internal glands with granular material in each side of post-proventricular setigers, two to three per parapodium. Pygidium small, anal cirri longer than dorsal cirri, thick, rectangular to oval (Fig. 1D). Pharynx thin, with distinct sinuation, through about 3 segments (Fig. 1A, B); trepan with 20 similar acutely triangular teeth (Fig. 1C). Proventriculum shorter than pharynx, through about 1½ segments, with 22 muscle cell rows (Fig. 1A, B). Reproduction unknown.

Remarks.—The only species of Autolytinae in the Mediterranean with only simple setae is *Procerastea pori* Ben-Eliahu, 1977 (Ben-Eliahu 1977, San Martín 1984); however, this species has setae very different in shape, the trepan has only five large teeth, lacks of bayonet setae and nuchal epaulettes and, finally, the real number of tentacular cirri is unknown.

Key to the genera of Autolytinae

The genera *Autosyllis* and *Odontoautolytus* are not included in the key for the reasons given in the remarks.

1. Pharynx unarmed 2
– Pharynx provided with a trepan ... 3
2. Two pairs of tentacular cirri. Occip-

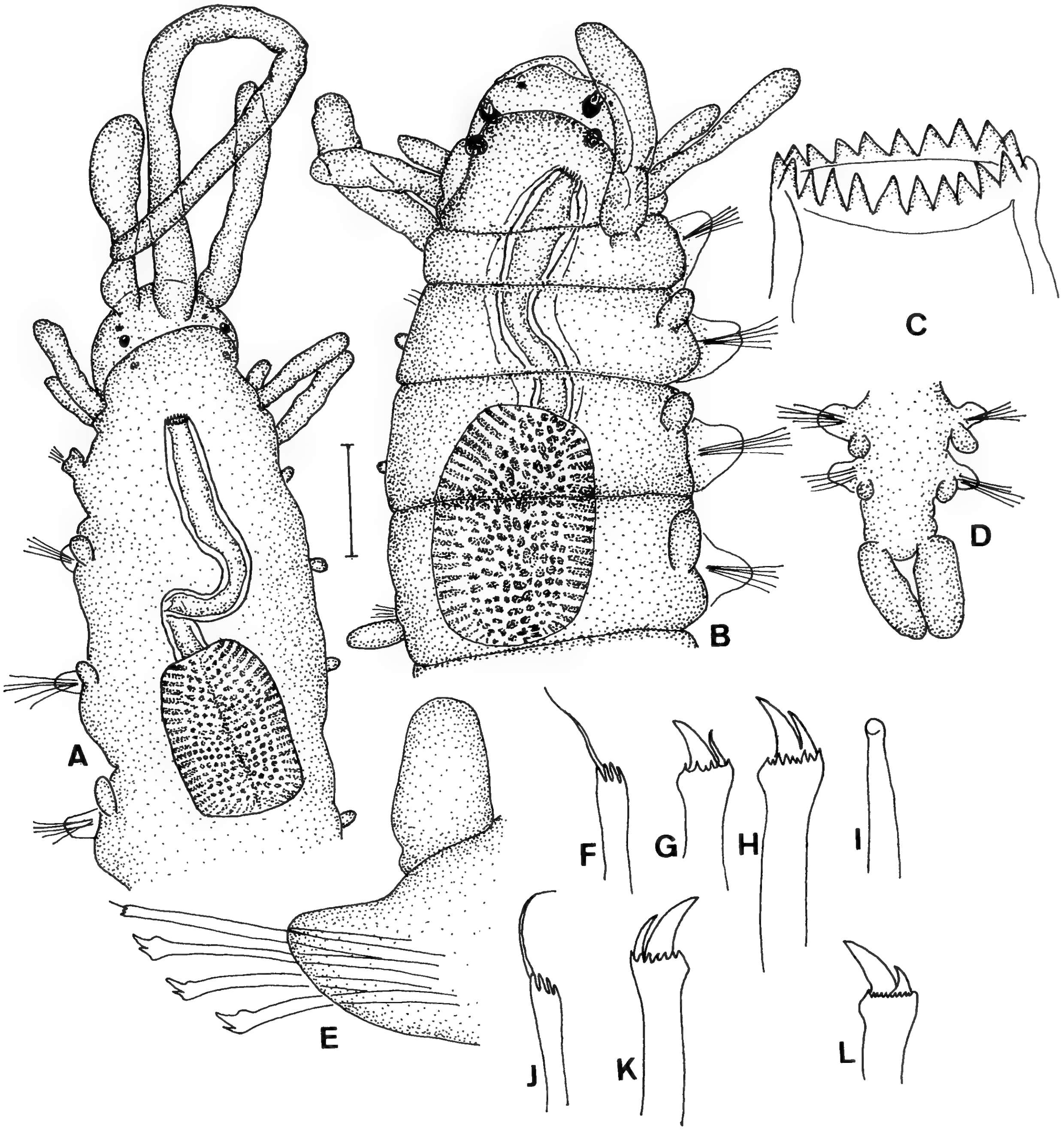

Fig. 1. *Paraprocerastea crocantinae,* gen. and sp. n. A, Anterior end, dorsal view, holotype; B, Anterior end, dorsal view, paratype from Almería; C, Trepan; D, Posterior end, dorsal view, paratype from Almería; E, Middle-posterior parapodium, paratype from Almería; F, J, Bayonet-shaped setae; G, H, K, L, Simple setae; I, aciculum. Scale: A, B, D: 0.13 mm; E: 20 μm; C, F, G, H, I, J, K, L: 10 μm.

ital flap present. Dorsal cirri well developed, similar throughout. Falcate simple setae or compound setae .... *Alluaudella* Gravier, 1905

– One pair of tentacular cirri (?). No occipital flap. Dorsal cirri from setiger 2 small, pyriform. Compound setae .... *Phyllosyllis* Ehlers, 1897

3\. Dorsal cirri only on first setiger of the atokous stock (stolons with very small dorsal cirri on all segments) .... *Procerastea* Langerhans, 1884

– Dorsal cirri throughout in the atokous stocks 4

4\. Anterior appendages club-shaped, dorsal cirri from setiger 2 minute, egg-shaped. Only simple setae. Occipital flap present .... *Paraprocerastea* n. gen.

– Anterior appendages cylindrical,

club-shaped or foliaceous, dorsal cirri longer, not egg-shaped. No occipital flap; two nuchal epaulettes. Compound setae and simple bayonet setae 5
5. Dorsal cirri cylindrical 6
– Dorsal cirri club-shaped or foliaceous 7
6. Bayonet setae as thick as shafts of compound setae. Without body ciliation ...... *Proceraea* Ehlers, 1864
– Bayonet setae more slender than shafts of compound setae. Segmentalciliary bands .... *Autolytus* Grube, 1850
7. Dorsal cirri foliaceous. Two short ciliated nuchal epaulettes .... *Myrianida* Milne Edwards, 1845
– Dorsal cirri club-shaped. Two very long, ciliated, foliaceous nuchal epaulettes .... *Umbellisyllis* Sars, 1869

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FOUR NEW WEST ATLANTIC SPECIES OF *TUBIFICOIDES* (OLIGOCHAETA, TUBIFICIDAE)

Christer Erséus

Abstract. —Two species without hair setae are described from the Caribbean area: *Tubificoides panamensis,* from Panama and Bahamas, and *T. inops,* from Panama, Barbados and the Gulf of Mexico. The former is closely related to *T. motei* Brinkhurst, 1986 from Florida, but differs in setal numbers, shape of penis sheaths and morphology of spermathecal ducts. The latter lacks true penes and penis sheaths, but is included in *Tubificoides* as its genitalia in all other respects share apomorphies with those of all other species of that genus. *Tubificoides bruneli,* and *T. crinitus,* both with hair setae, are described from Lower St. Lawrence estuary (Québec, Canada) and the Gulf of Mexico, respectively. The first species has very stout spermatozeugmata, and ventral setae in anterior segments with upper teeth much longer than lower. *Tubificoides crinitus* is a small species occurring on the continental slope (down to at least about 550 m); its dorsal setae are all hair-like (alternating long and short within bundles). The generic definition of *Tubificoides* Lastockin, 1937 is emended, partly to accommodate the aberrant *T. inops.*

The marine tubificid genus *Tubificoides* Lastockin, 1937 has been subject to recent revision by Brinkhurst (1985, 1986), with subsequent additions to the list of species by Råsmark & Erséus (1986), Helgason & Erséus (1987), Milligan (1987), Erséus & Milligan (1989), Erséus (1989), and Erséus & Davis (1989). The present contribution describes four additional species of this large genus. Two of them possess, the other two lack hair setae in their dorsal bundles.

The material comes from (1) the author's own collection in Barbados (while at the Bellairs Research Institute of McGill University); (2) material from R.V. *Alpha Helix* cruise "CARIB. I." in 1977 (sorted by Smithsonian Oceanographic Sorting Center, SOSC, Washington, D.C.); (3) a collection from Andros Island, Bahamas [courtesy Dr. M. L. Jones, United States National Museum of Natural History (USNM), Washington, D.C.]; (4) samples from off Pascagoula, Mississippi, in the northern Gulf of Mexico (courtesy Mr. M. R. Milligan, Mote Marine Laboratory, Sarasota, Florida); (5) oligochaetes from the St. Lawrence estuary, Québec (courtesy Prof. P. Brunel, Université de Montréal, Montréal, Québec, Canada); and (6) benthos from a study of the Northern Gulf of Mexico Continental Shelf (LGL Ecological Research Associates, Inc., Bryan, Texas, for Minerals Management Service).

Material collected by the author was fixed in Bouin's fluid, that collected by colleagues probably in formalin for most parts. Some specimens of *T. inops* were longitudinally sectioned and stained in Heidenhain's hematoxylin, all other worms were stained in paracarmine and mounted whole in Canada balsam. The type series are all deposited in the USNM.

Tubificoides panamensis, new species
Fig. 1

Holotype. —USNM 119870, whole-mounted specimen from N coast of

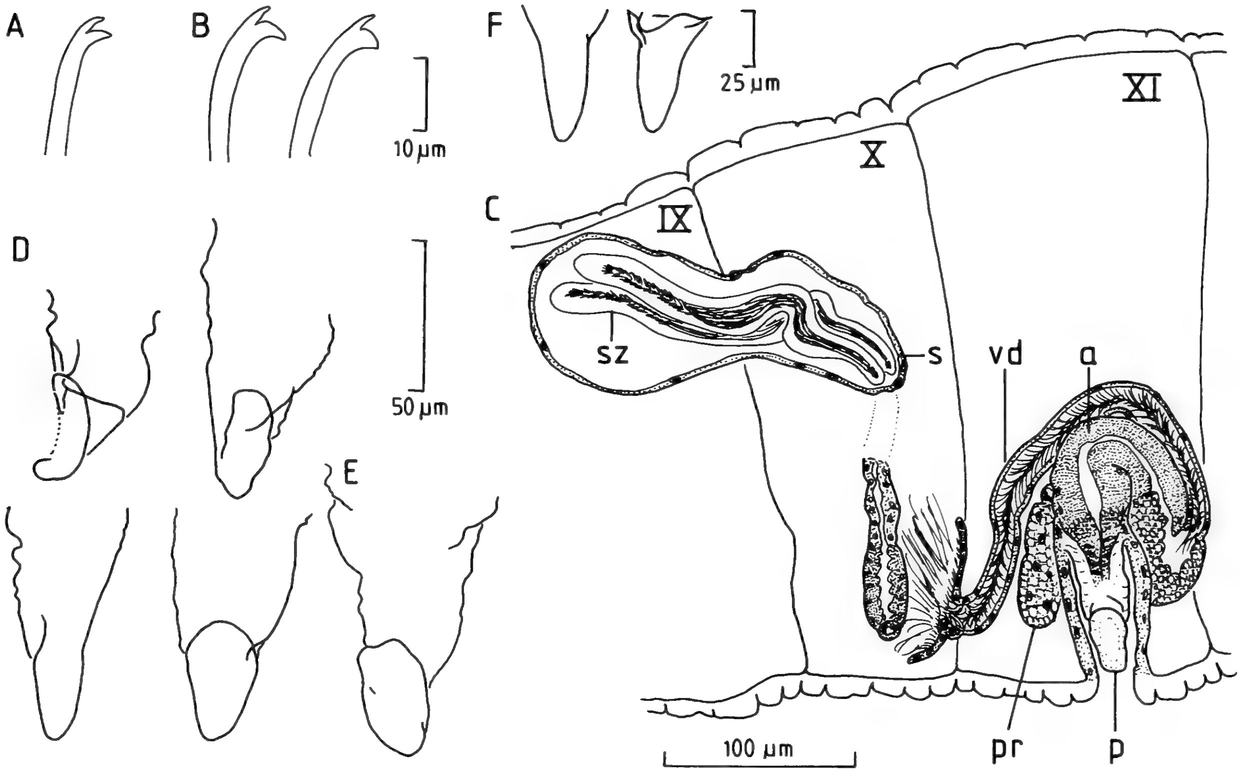

Fig. 1. A–E, *Tubificoides panamensis*: A, Anterior seta; B, Posterior setae; C, Lateral view of spermatheca and male genitalia in segments (IX)X–XI; D, Penis sheaths, specimens from Panama; E, Penis sheath, specimen from Bahamas; F, *Tubificoides motei* Brinkhurst: penis sheaths, specimens from Miami, Florida (coll. by author in 1977). Abbreviations: a, atrium; p, penis; pr, prostate gland; s, spermatheca; sz, spermatozeugma; vd, vas deferens.

Panama, Caribbean Sea, 90°34′36″N, 78°43′12″W, 0–4 m (30 Jun 1977); CARIB. I. *Alpha Helix* Stn. no. 23-333/149.

Paratypes.—USNM 119871–119873, three specimens from type locality. USNM 119874, one specimen from High Ridge Cay, Andros Island, Bahamas, 24°17′42″N, 77°45′12″W, subtidal, associated with *Thalassia* (5 Mar 1966); M. L. Jones Stn. no. 56.

Description.—Length 4.7–8.7 mm, up to 49 segments (some specimens not fully differentiated posteriorly). Width at XI 0.35–0.44 mm. Prostomium small, triangular. Postclitellar segments often elongate. Body wall naked anteriorly, with cover of particles tending to form papillae on small cuticular projections in postclitellar segments. Clitellum extending over XI–½XII. Setae all bifid, 45–65 µm long, two (rarely three) per bundle throughout most of body (generally reduced to one per "bundle" in clitellar region and near posterior end), with upper tooth thinner and slightly shorter than lower; teeth more diverging in postclitellar (Fig. 1B) than in anterior setae (Fig. 1A), with lower tooth occasionally much longer than upper. Ventral, and generally also dorsal, setae absent from XI. Spermathecal pores in middle of X, between lateral lines and lines of ventral setae. Male pores in line with ventral setae in middle of XI.

Pharyngeal glands in IV–V. Esophagus somewhat enlarged in IX. Male genitalia (Fig. 1C) paired. Vas deferens 17–21 µm wide, thin-walled and ciliated, about 1.5 times longer than atrium, entering latter subapically opposite to entrance of prostate gland. Atrium small and curved, histologically tri- or bipartite (third, most ectal region not always distinct), about 165–175 µm long, entally 40–47 µm wide, at middle 23–33 µm wide, ectally 40–47 µm wide, with very thin outer lining of muscles. Ental part of atrium heavily granulated; granulation similar to that of prostate gland. A short, granulated portion generally also discernible in ectal part of atrium, at base of penis. Prostate gland small, without discrete stalk. Penis (Figs. 1C, p; D–E) with cuticularized, conical penis sheath, with somewhat irregular, wrinkled outline and large oval lateral opening. Penis 65–95 μm long, basally 35–55 μm wide, at opening 16–28 μm wide. Spermathecae (Fig. 1C, s) with slender, 80–105 μm long, 23–20 μm wide ducts, and elongate ampullae; ectal half of ducts thickened and somewhat glandular, ampullae with slender spermatozeugmata.

Remarks.—*Tubificoides panamensis* appears closely related to *T. motei* Brinkhurst, 1986, known from Florida, but differs from that species by: (1) its lower number of setae (two, only rarely three, per bundle, as opposed to three, or even four, per bundle in anterior segments of *motei*); (2) its less smoothly funnel-shaped penis sheaths, which exhibit very distinct lateral openings [penis sheath openings not as distinct in specimens of *motei* from Miami in my possession (see Fig. 1F); it should be noted, however, that according to Brinkhurst (1986: 1274, fig. 3), the narrow distal end of the penis sheath of *motei* is "possibly with an oblique opening"]; and (3) the thickened ectal halves of the spermathecal ducts (ducts ectally provided with a very short, round and hollow swelling in my material of *motei*).

Distribution and habitat.—Caribbean side of Panama, Bahamas. Subtidal to about 4 m depth. In Panama, the species was found together with *T. inops.*

Tubificoides inops, new species
Fig. 2

Holotype.—USNM 119875, whole-mounted specimen from N coast of Panama, Caribbean Sea, 09°34′36″N, 78°43′12″W, 0–4 m (30 Jun 1977); CARIB I. *Alpha Helix* Stn. no. 23-333/149.

Paratypes.—USNM 119876–119880, five whole-mounted specimens from type locality. USNM 119881–119885, one sectioned and four whole-mounted specimens from "the hole," at Holetown, St. James, Barbados, 5–9 m, muddy silt (28 Oct to 1 Nov 1979; C. Erséus).

Other material.—Author's collection: two sectioned and seven whole-mounted specimens from Carlisle Bay, Barbados, 3.5–6.5 m, muddy silt and sand (24–25 Oct 1979; C. Erséus); and three sectioned and five whole-mounted specimens from Holetown (see paratypes). M. R. Milligan collection: two whole-mounted specimens (one of which sexually immature) from off Pascagoula, Mississippi, northern Gulf of Mexico, 30°11′42″N, 88°37′18″W, 13 m, medium to fine sand with silt and clay (22 Apr 1987).

Etymology.—The name *inops* is Latin for "poor, lacking," alluding to the species' lack of penes.

Description.—Length 3.1–6.6 mm, 24–45 segments; width at XI 0.23–0.42 mm. Prostomium small, generally rounded and shorter than wide; posterior segments often elongate. Body wall naked anteriorly, in postclitellar segments with cover of fine particles, generally aggregated into discrete, pointed papillae. Clitellum extending over XI–½XII. Setae all bifid, 50–75 μm long, two to five per bundle anteriorly, one to three per bundle in postclitellar segments, with upper tooth thinner than lower; upper tooth somewhat longer than lower and lower tooth bearing indistinct subdental ligament in anterior setae (Fig. 2A), upper tooth shorter than lower in postclitellar setae (Fig. 2B). Ventral setae sometimes absent from XI. Spermathecal pores immediately anterior to ventral setae, in middle of X; male pores paired in line with ventral setae in middle of XI.

Pharyngeal glands in IV–V. Esophagus somewhat enlarged in IX. Male genitalia (Fig. 2D–E) paired; vas deferens 8–13 μm wide, thin-walled and ciliated, about 1.5

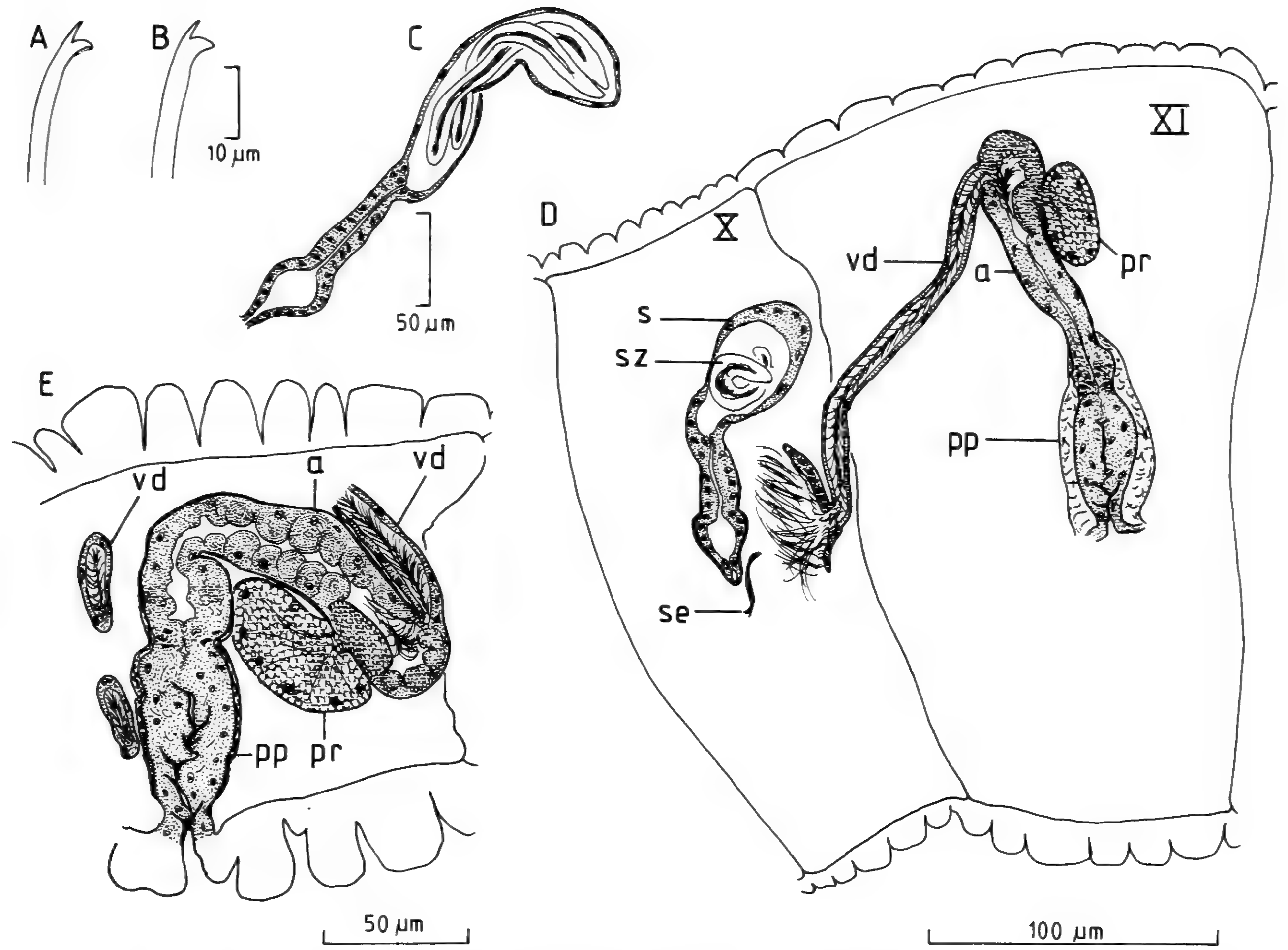

Fig. 2. *Tubificoides inops*: A, Anterior seta; B, Posterior seta; C, Spermatheca, specimen from Barbados; D, Lateral view of spermatheca and male genitalia in segments X–XI, whole-mounted specimen from Panama; E, Lateral section through male genitalia in segment XI, sectioned specimen from Barbados. pp, pseudopenis; se, seta; other abbreviations as in Fig. 1.

times longer than atrium, entering latter subapically opposite to entrance of prostate gland; atrium erect or curved, histologically tri- or bipartite (third, most ectal region not always distinct), 80–145 μm long, entally 23–40 μm wide, at middle 11–35 μm wide, ectally 21–39 μm wide, with about 1–2 μm thick outer lining of muscles; ental part of atrium granulated in a way different from that of other parts, sometimes some distinct granules also discernible in ectal part of atrium, at base of pseudopenis. Prostate gland compact, small, with smooth outline. True penis absent, instead copulatory sac, 35–65 μm long, 33–45 μm wide, modified into an (eversible?) pseudopenis; inner surface of sac lined with cuticle and folded in an irregular way. Spermathecae (Fig. 2C; D, s) slender, with 55–115 μm long, 20–34 μm wide ducts, and thin-walled ampullae, ducts with roundish ectal swelling, ampullae containing slender spermatozeugmata.

Remarks.—The specimens from the type locality (Panama) have genitalia that are clearly smaller (Fig. 2D) than those of the worms from Barbados (Fig. 2C, E) and Gulf of Mexico.

The copulatory organs of *T. inops* are different from those of all congeners; they are pseudopenes rather than true, pendant penes. In fact, this feature disqualifies it for inclusion in the genus as currently defined (Brinkhurst & Baker 1979:1554): ". . . penial structure bearing a penis sheath of varying form." However, its body wall papillation, characteristic atria and spermathecae appear to be good synapomorphic characters shared with all "typical" members of *Tubificoides.* Then *T. inops* is either a very primitive member of the group (true penes had still not evolved when *inops,* or its ancestor, was split off from the rest of the lineage), or it is an advanced species within *Tubificoides* in the sense that its copulatory structure has "regressed" to an eversible pseudopenis. In the first case, *T. inops* could be hypothesized as the plesiomorphic sister group to the others and could be regarded as a monotypic genus, separate from *Tubificoides.* In the second case, it should (cladistically) be classified as a *Tubificoides.* Since most Tubificinae possess true penes, but do not possess the particular (advanced) atria fround in *T. inops* (and in *Tubificoides* as a whole), the latter alternative seems the most parsimonious one.

Accordingly, the generic definition of *Tubificoides* is modified below to accommodate also *T. inops.*

Distribution and habitat.—Caribbean coast of Panama, Barbados, Gulf of Mexico. Subtidal silt and sand, to at least 13 m depth. In Panama, the species was found together with *T. panamensis.*

Tubificoides bruneli, new species
Fig. 3

Holotype.—USNM 119886, whole-mounted specimen from off Ile du Bic, Lower St. Lawrence estuary, Québec, Canada, 48°26′24″N, 69°00′00″W, 242 m, silt (31 Jul 1970; P. Brunel).

Paratypes.—USNM 119887–119890, four specimens from type locality.

Other material.—Author's collection: three specimens from type locality.

Etymology.—The species is named for Prof. P. Brunel (Département de Biologie, Université de Montréal), who provided the material.

Description.—Length more than 7.6 mm, more than 63 segments (no complete specimens available); width at XI 0.37–0.50 mm. Prostomium variable in shape, rounded or triangular. Body wall with some scattered particles in postclitellar segments. Clitellum extending over XI–½XII. Dorsal bundles of II–VIII containing two to three bifid setae (Fig. 3A), up to 85 μm long and with parallel, more or less equally long, slender teeth, and two hair setae, up to 200 μm long; from IX, dorsal bundles containing one bifid or single-pointed seta (Fig. 3B), up to 85 μm long, if bifid with teeth small and upper tooth longer than lower, and one hair, up to 145 μm long. Ventral bundles of II–VIII with two to three bifid or single-pointed setae (Fig. 3C), up to 105 μm long; if bifid, teeth slender and upper tooth much longer than lower; from IX, ventral setae single-pointed, up to 85 μm long, one to two per bundle; ventral setae absent from XI. Spermathecal pores anterior to, and at some distance from, ventral setae, anterior to middle of X; male pores in line with ventral setae, posterior to middle of XI.

Pharyngeal glands in IV–V. Esophagus not particularly enlarged in IX. Male genitalia (Fig. 3E) paired; vas deferens 16–22 μm wide, thin-walled and ciliated, several times longer than atrium, but exact length not established. Entrance of vas into atrium not observed, but probably subapical as in all congeners; atrium curved, histologically tripartite, 340–430 μm long, entally 60–70 μm wide, at middle 50–65 μm wide, ectally 50–90 μm wide, with thin outer lining of muscles; ental and ectal parts of atrium granulated in a way different from that of middle part. Prostate gland large, lobed. Penis (Fig. 3D; E, p) with cuticularized, smooth, funnel-shaped penis sheath with ectal ends characteristically distended and curved (opening terminal), 105–120 μm long, basally 50–65 μm wide, at distended ectal ends 28–42 μm wide. Spermathecae (Fig. 3E, s) with 70–80 μm long, 41–47 μm wide ducts, and thin-walled, roundish ampullae; ducts with oval ectal swelling, lumen of which

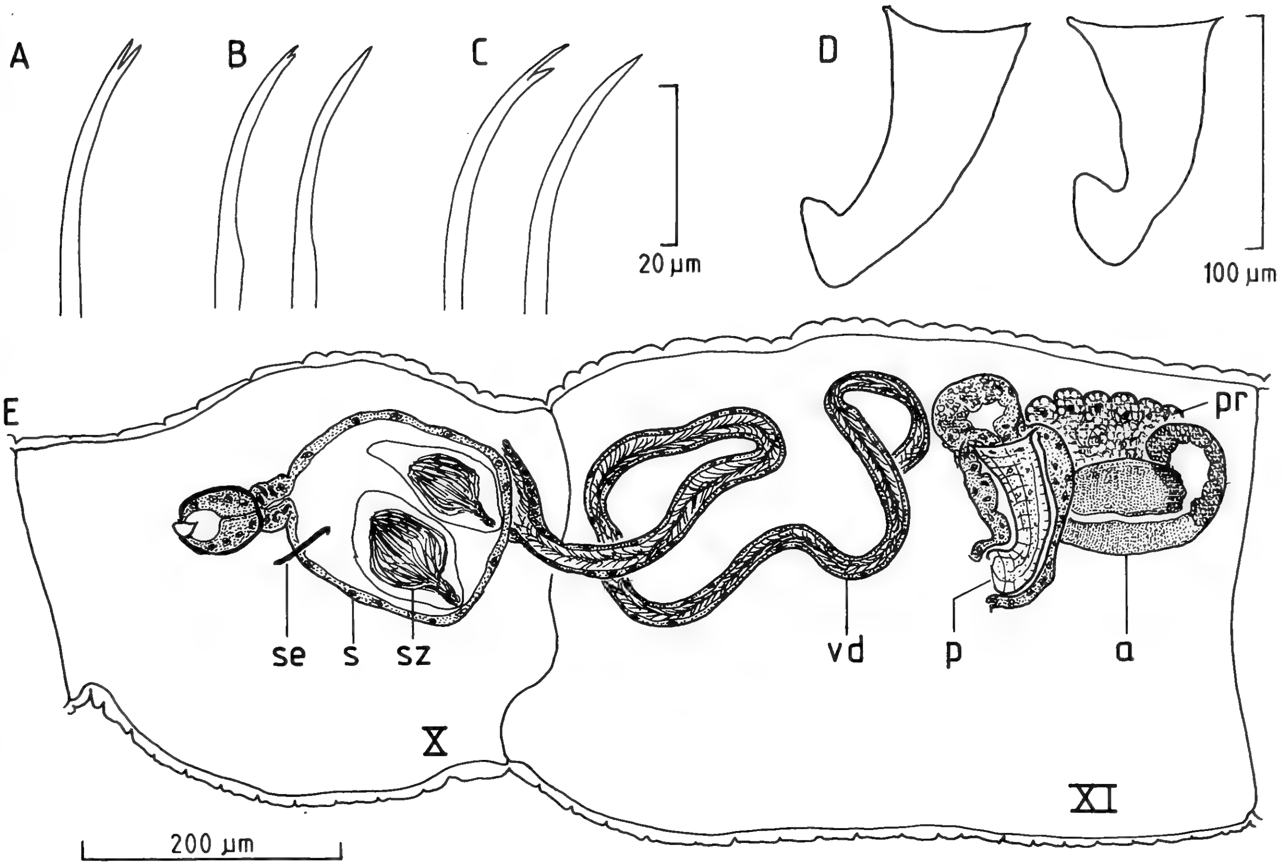

Fig. 3. *Tubificoides bruneli*: A, Dorsal anterior seta; B, Dorsal postclitellar setae; C, Ventral anterior setae; D, Penis sheaths; E, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations as in Figs. 1–2.

hollow near pore, ampullae with very stout, or (in one paratype only) slender, spermatozeugmata (Fig. 3E, sz).

Remarks.—Only two additional species in the genus have single-pointed ventral setae in postclitellar segments, viz., *T. palacoleus* Baker, 1983 and *T. cuspisetosus* Baker, 1983. The new species is, however, easily distinguished from both of these by its very characteristic penis sheaths; the penes are straight in the other two, those of *T. palacoleus* being provided with a strongly flared tip, those of *T. cuspisetosus* being very slender. The shape of the penis sheaths (Fig. 3D), as well as the very long upper tooth of at least some of the anterior ventral setae (Fig. 3C), in fact distinguish *T. bruneli* from all congeners. The similarities in the outline of the penis sheaths with that found in *T. crenacoleus* Baker, 1983 is superficial; whereas the tip of the sheath is properly curved in *T. bruneli,* it is more or less straight, but bears a lateral, blunt projection, in *T. crenacoleus.*

The very stout spermatozeugmata found in all but one of the postcopulatory specimens in the available material (spermatozeugmata of "normal," slender type found in one worm only) are also noteworthy; spermatozeugmata with a similar shape have previously only been reported for *T. aculeatus* (Cook, 1970) (cf. Cook 1970: fig. 2D).

Distribution and habitat.—Known only from the type locality in the St. Lawrence estuary, Canada. Subtidal, silty sediment, 242 m depth.

Tubificoides crinitus, new species
Figs. 4–5

Holotype.—USNM 119891, whole-mounted specimen from S of Louisiana,

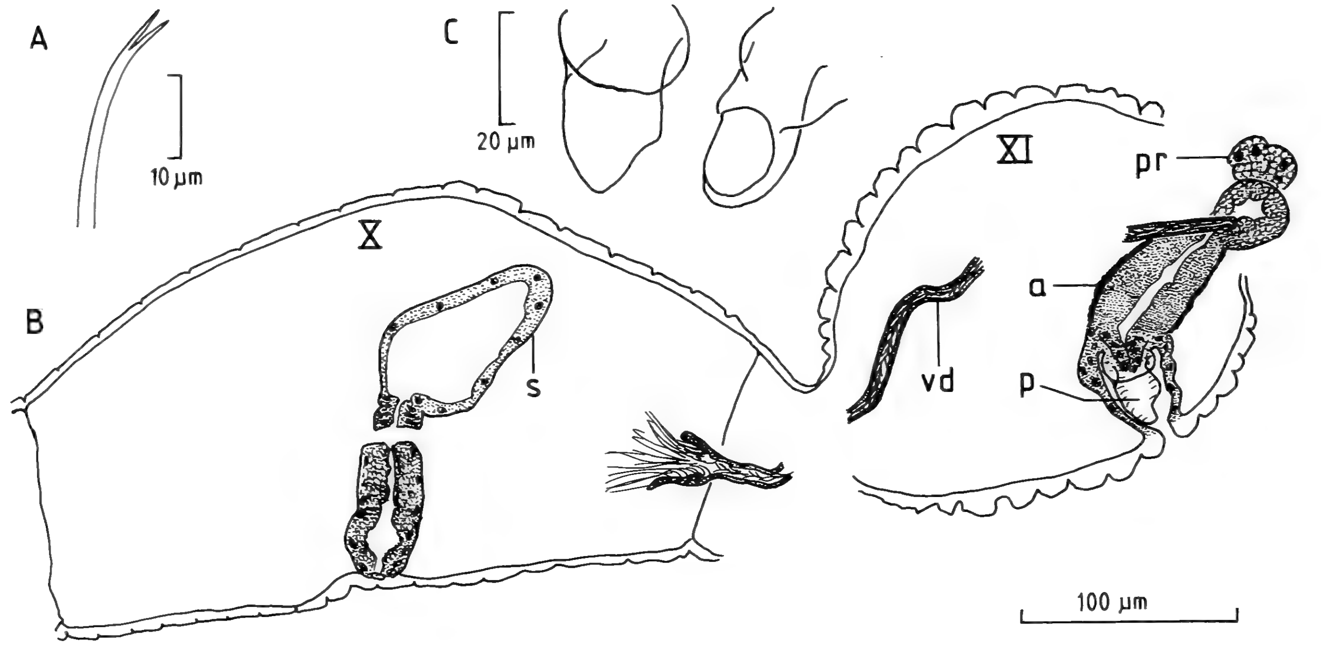

Fig. 4. *Tubificoides crinitus,* holotype: A, Ventral anterior seta; B, Lateral view of spermatheca and male genitalia in segments X–XI; C, Penis sheaths. Abbreviations as in Fig. 1.

27°43′07″N, 92°53′18″W, 349 m (Minerals Management Service, Northern Gulf of Mexico Continental Shelf Study; 7 Jun 1985).

Paratypes.—USNM 119892–119895, four specimens: one from type locality; one from 27°43′23″N, 92°53′23″W, 335 m (7 Jun 1985); one from 27°50′29″N, 90°44′06″W, 547 m (13 Jun 1985); and one (immature) from 28°34′42″N, 90°14′06″W, 320 m (26 Nov 1983).

Etymology.—The name *crinitus* is Latin for "having hair, hairy," referring to the species' possession of hair-like setae throughout the dorsal bundles.

Description.—Length and segment number unknown (specimens not complete), but worms appear very small. Width at XI 0.13–0.22 mm. Prostomium small, blunt, at least partially retractable. Body wall naked anteriorly, with some fine particles in postclitellar segments (but very few postclitellar segments remain on available worms). Clitellum poorly developed. Anterior dorsal bundles with one to three hair-like, single-pointed crotchets, 65–85 µm long, and one to three hair setae, 125–175 µm long; postclitellar dorsal bundles with two short hair-like setae, one slightly longer than the other; ventral bundles with (one) two to three bifid setae (Fig. 4A), 60–80 µm long, with very slender, thin and almost parallel teeth; teeth equally long. Ventral setae of XI absent. Spermathecal pores in line with (and near) ventral setae in middle of X; male pores in line with ventral setae slightly posterior to middle of XI.

Pharyngeal glands in IV–V. Esophagus somewhat enlarged in IX. Male genitalia (Figs. 4B, 5) paired; vas deferens 8–11 µm wide, thin-walled and ciliated, at least about three times longer than atrium, entering latter subapically. Atrium of varying shape and length, histologically bi- or tripartite, 80–185 µm long, 30–42 µm wide, with up to 3 µm thick lining of (circular) muscles; ental part of atrium heavily granulated, remaining part less so. Prostate gland small, appears to be attached to atrium at some distance from apical end (see Fig. 5). Penis (Figs. 4B, p; C; 5, p) with cuticularized, cone-shaped penis sheath possessing large subterminal opening; penis 37–47 µm long, basally 23–26 µm wide, ectally 16–19 µm wide. Spermathecae (Fig. 4B, s) with 65–95 µm long, 28–36 µm wide ducts, and roundish to oval, small ampullae; ducts appear glandular, each with a roundish and hollow ectal swelling; ampullae empty in holotype, with a few poorly preserved, slender, spermatozeugmata in one paratype.

Remarks.—Two other species of *Tubificoides* lack bifid setae throughout the dorsal bundles: *T. aguadillensis* Milligan, 1987, from Puerto Rico, and *T. uncinatus* Helgason & Erséus, 1987, from off the east coast of the U.S.A. These species, as well as *T. crinitus,* are also characterized by the somewhat aberrant location of the prostate gland on the atrium; the prostate is not attached to atrium opposite to entrance of vas deferens, but at a considerable distance from the apical end of the atrium (cf. Milligan 1987:fig. 4C; Helgason & Erséus 1987:fig. 6A). Both *T. aguadillensis* and *T. uncinatus* differ, however, from *T. crinitus* by having bifid (ventral) setae with short, i.e., "normal," teeth, and the penis sheaths of *T. aguadillensis* are evenly conical with a small terminal opening (penis sheaths of *crinitus* not as evenly tapering and with a large subterminal opening), those of *T. uncinatus* are long and cylindrical and provided with a large subapical spur.

The spermathecae of the available material of *T. crinitus* are smaller and with stouter ducts and ampullae than those of most other species of the genus. However, as most of the studied specimens are precopulatory, this feature should be used with some caution; other, postcopulatory, worms of *T. crinitus* may have larger spermathecae than those described here.

A species very similar to *T. crinitus* is simultaneously described from a hydrocarbon seep area in the northern Gulf of Mexico by Erséus & Milligan (1989).

Distibution and habitat.—Known only from the northern Gulf of Mexico. Subtidal on outer part of continental shelf, 320–547 m depth.

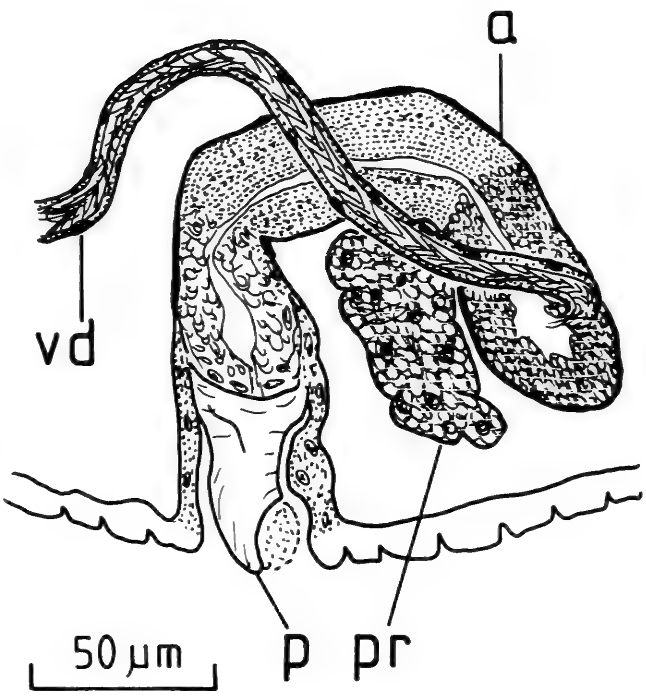

Fig. 5. *Tubificoides crinitus,* paratype: male genitalia. Abbreviations as in Fig. 1.

Tubificoides Lastockin, 1937

Definition (emended).—A species-rich group of marine and brackish-water tubificids (subfamily Tubificinae). Body wall naked, or with fine particles adhering to cuticle, often forming distinct papillae. In most heavily papillated species, prostomium often retractable. Hair setae absent or present in dorsal bundles; when present, generally together with single-pointed, bifid or pectinate crotchets. Posterior dorsal setae, at least, frequently reduced to a single-pointed form barely distinguishable from the short hair setae where these are present. Modified genital setae absent. Male pores paired, more or less in line with ventral setae in posterior part of segment XI. Spermathecal pores paired more or less in middle of X.

Coelomocytes, if present, small and sparse, not of the "rhyacodriline-type." Male efferent ducts paired in XI. Vas deferens ciliated, thin-walled, entering atrium subapically, generally opposite to large prostate gland. Rounded inner end of atrium caplike, very heavily granulated and histologically different from rest of atrium. Main body of atrium cylindrical, generally curved; terminal part often again histologically distinct. Atrium terminating in a copulatory sac, which in all but one species contains a pendant penis bearing a cuticular penis sheath (in *T. inops* the copulatory organ is modified into a complex, probably eversible, pseudopenis). Spermathecae consisting of a cylindrical duct, which often bears a distinct swelling near the ectal pore, and a round or oval-to-pear-shaped ampulla. Latter with spindle-shaped, often very slender, spermatozeugmata in postcopulatory specimens.

Type species.—*Tubificoides heterochaetus* Lastockin, 1937 = *T. swirencowi* Jaroschenko, 1948 [not *T. heterochaetus* (Michaelsen, 1926)] (see Brinkhurst & Baker 1979).

Remarks.—This definition is an extended and partly revised version of the latest one by Brinkhurst & Baker (1979:1554). The shape of the atrium (with the cap-like apical part and the subapical entrance of the vas deferens) should probably be regarded as the single most important synapomorphy for the genus. This is why *T. inops,* which lacks proper penes, is included (see further Remarks for *T. inops* above).

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THREE NEW SPECIES OF TUBIFICIDAE (OLIGOCHAETA) FROM AN OIL SEEPAGE AREA ON THE CONTINENTAL SLOPE OF THE NORTHERN GULF OF MEXICO

Christer Erséus and Michael R. Milligan

Abstract.—*Limnodriloides olearius* (subfamily Limnodriloidinae), *Tubificoides paracrinitus,* and *T. pequegnatae* (Tubificinae) are described from a hydrocarbon seep area of vestimentiferan growth at 540 m depth south of Louisiana. The tubificids are associated with vestimentiferans, mussels and bacterial mats. *Limnodriloides olearius* belongs to the *winckelmanni*-group within the genus, but is unique by its possession of transverse patches of epidermal glands ventrally in segments III–X. *Tubificoides paracrinitus* is closely related to *T. crinitus* Erséus, 1989, but is larger and possesses postclitellar body wall papillae, a greater number of setae, and different penes and spermathecae; *T. pequegnatae* resembles *T. bakeri* Brinkhurst, 1985 in its setal distribution, but differs in the morphology of its penis sheaths.

Five samples of oligochaetes, from an area of natural hydrocarbon seepage on the Gulf of Mexico continental slope about 128 km south of Louisiana, were sent to the senior author for identification. They represented three new species of Tubificidae (one species of *Limnodriloides* Pierantoni, two of *Tubificoides* Lastockin) described in the present paper.

The samples were collected from the submersible *Johnson Sea Link I,* Dive No. 1878 (28 Sep 1986), at "Bush Hill," an area of thick growths of tube worms, mussel beds and bacterial mats in Blocks 184 and 185 of the Green Canyon offshore oil leasing area (cf. Brooks et al. 1987); oil leasing blocks being set by the U.S. Department of Interior, Minerals Management Service. The worms were provided by LGL Ecological Research Associates, Inc. (Bryan, Texas). Only two or three sexually mature individuals of each species were found. The specimens were stained in paracarmine and mounted whole in Canada balsam, and have been deposited as type specimens in the U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Subfamily Limnodriloidinae

Limnodriloides olearius, new species
Fig. 1.

Holotype.—USNM 119904, 2.4 mm long, consisting of first 15 segments only, from S of Louisiana, 27°46′56″N, 91°30′20″W, 540 m (28 Sep 1986), in area of vestimentiferan growth.

Paratype.—USNM 119905, from type locality.

Etymology.—The epithet *olearius* is Latin for "of oil," here alluding to the species' occurrence in an area of oil seepage.

Description.—Length more than 4.2 mm, more than about 35 segments (no specimen complete); width at XI in whole-mounted, compressed specimens about 0.25 mm. Prostomium rounded triangular. Clitellum not distinct in available specimens. Very distinct, transverse, elongated patches of epidermal glands present ventrally in most of preclitellar segments, at least in III–X

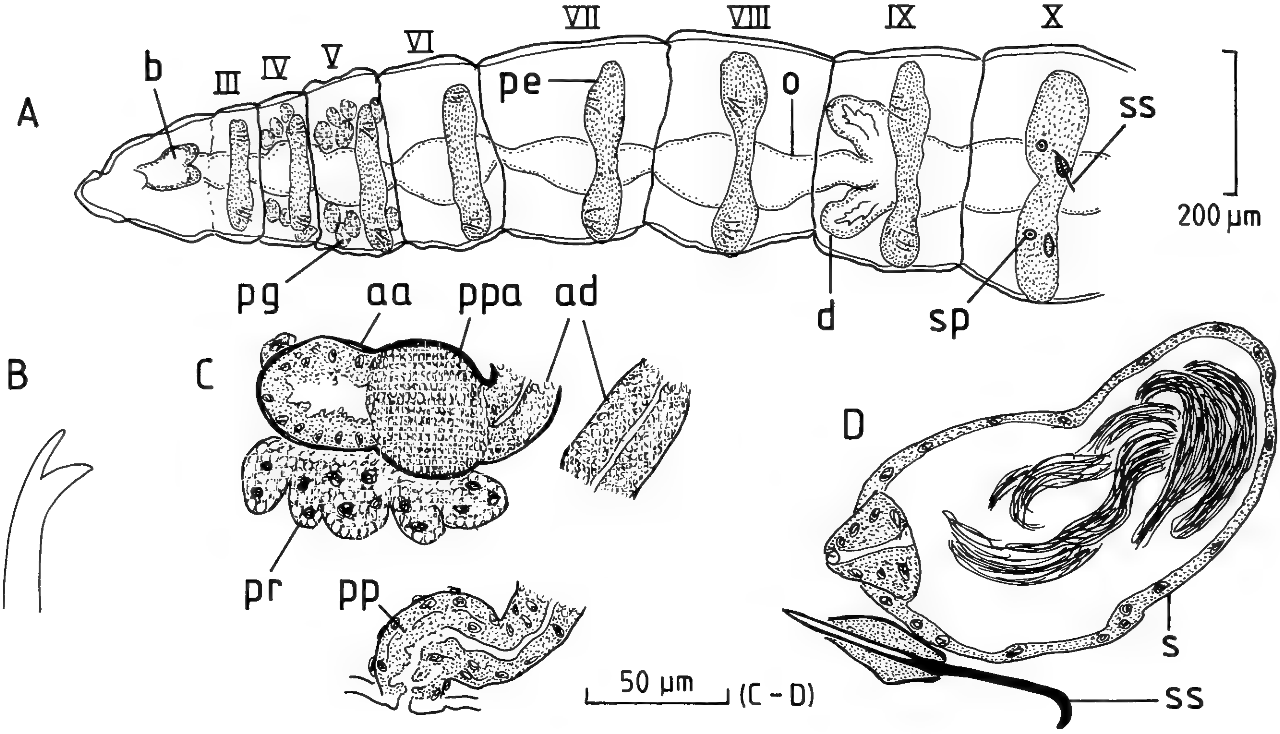

Fig. 1. *Limnodriloides olearius,* n. sp.: A, Ventral view of anterior end of worm (semi-schematical); B, Free-hand drawing of somatic seta; C, Three (probably all) parts of one atrium, holotype; D, Spermatheca and spermathecal seta. Abbreviations: *aa* atrial ampulla; *ad* atrial duct; *b* brain; *d* oesophageal diverticula; *o* oesophagus; *pe* patch of epidermal glands; *pg* pharyngeal glands; *pp* pseudopenis; *ppa* prostatic pad; *pr* prostate gland; *s* spermatheca; *sp* spermathecal pore; *ss* spermathecal seta; Roman numerals denoting segment numbers.

(Fig. 1A, pe); bundles of ventral setae and (in X) spermathecal pores located within these glandular patches. Somatic setae (Fig. 1B) bifid, with upper tooth as long as but thinner than lower; bifids 40–70 μm long, about 2.5 μm thick, (two) three (four) per bundle anteriorly, two per bundle in postclitellar segments. In holotype and paratype, one spermathecal seta (Fig. 1D, ss), partly enclosed in narrow (glandular?) sac, present immediately posterior to one of the two spermathecal pores in X; at other side of X setal sac empty (spermathecal seta lacking; see Fig. 1A). Spermathecal seta, single-pointed, shaped like a walking-stick, about 100–110 μm long, about 3.5 μm at node, with node at about middle, and with part ectal to node grooved; large gland associated with sac of spermathecal seta not observed, but may be present (as in some congeners; see, e.g., Erséus 1982:figs. 15, 20–21). Penial setae absent; male pores paired, somewhat ventral to lines of ventral setae, in middle-to-posterior part of XI; spermathecal pores paired, in line with ventral setae, in middle of X.

Pharyngeal glands (Fig. 1A, pg) present in IV–V. Large, somewhat conical esophageal diverticula (Fig. 1A, d) present in IX. Male genitalia (Fig. 1C) paired, not well preserved in available material; vas deferens 9–14 μm wide, but length and junction with atrium not established. Atrial ampulla 75–80 μm long, about 45 μm wide, with ectal half filled with large, conspicuous prostatic pad; muscular lining of ampulla 2–3 μm thick in paratype, thinner in holotype (Fig. 1C); prostate gland lobed. Atrial duct (broken into pieces in holotype; not visible in paratype) slender, about 135 μm long, 21–28 μm wide, granulated for most parts, terminating in simple pseudopenis with somewhat folded inner wall; inner structure of pseudopenis not clear, but no distinct pseudopenial papilla appears to be present. Spermathecae (Fig. 1D, s) large, consisting of very short, triangular ducts, and oval, up to about 170 μm long, 75 μm wide, ampullae;

sperm arranged as distinct, curved bundles in spermathecae; possibly they are (poorly preserved) spermatozeugmata.

Remarks.—The function of the conspicuous patches of epidermal glands in the anterior segments is unknown. It appears likely, however, that they are in some ways related to reproduction as such patches are not developed in four juvenile specimens of *Limnodriloides* found at the type locality, and presumably belonging to the same species. Patches of epidermal glands have not been reported for *Limnodriloides* before, and they are in fact distinguishing *L. olearius* from all other members of the subfamily Limnodriloidinae, but similar glands are present dorsally (largely in postclitellar segments) in some species of *Bathydrilus* Cook, in the subfamily Phallodrilinae (Erséus 1986:figs. 9A–B).

The new species is a member of the *winkelmanni*-group within *Limnodriloides,* i.e., the species with spermathecal setae (Erséus 1982). Both type specimens lack the spermathecal seta at one side of segment X, but this asymmetric arrangement is not necessarily a specific character; other species within the group occasionally lack one or both spermathecal setae (e.g., *L. victoriensis* Brinkhurst & Baker, 1979; see Brinkhurst & Baker 1979; Erséus 1982).

Among those species in the *winckelmanni*-group that have: (1) a pair of esophageal diverticula in segment IX, and (2) well separated male pores, *L. olearius* appears most closely related to *L. barnardi* Cook, 1974, a common species in the Northwest Atlantic and the Caribbean, and also known from the Pacific coast of Mexico; both species have elongate atrial ampullae with the prostatic pads located in the ectal half of these ampullae (Fig. 1C; Erséus 1982:fig. 13A). *Limnodriloides olearius* is distinguished from the latter by its shorter spermathecal ducts, and its very simple pseudopenes. In *L. barnardi,* the atrial ducts terminate in distinct pseudopenial papillae (Erséus 1982: fig. 13A–B), which in fact were erroneously interpreted as proper penes by the original author (Cook 1974). The male genitalia are not very well preserved in the material of *L. olearius,* but there is no indication of such discrete papillae in the copulatory organs (Fig. 1C, pp).

Distribution and habitat.—Only known from the type locality, N Gulf of Mexico. Upper continental slope, 540 m depth.

Subfamily Tubificinae

Tubificoides paracrinitus, new species

Fig. 2

Holotype.—USNM 119901, whole-mounted specimen from south of Louisiana, 27°47′01″N, 91°30′03″W, 582.5 m (28 Sep 1986), in area free of vestimentiferan growth, but not very far from the hydrocarbon seep.

Paratypes.—USNM 119902, 119903, two whole-mounted specimens from 27°46′56″N, 91°30′20″W, 540.1 m (28 Sep 1986), in area of vestimentiferan growth.

Etymology.—Named *paracrinitus* for its resemblance to *T. crinitus* Erséus, 1989.

Description.—Length of holotype 27.1 mm, 53 segments; paratypes not complete; width at XI in whole-mounted, compressed specimens 0.25–0.27 mm. Prostomium pointed triangular. Body wall naked anteriorly, but covered with very small papillae in most of postclitellar segments (papillation not beginning immediately behind clitellar region). Clitellum poorly developed. Anterior dorsal bundles with up to six hair-like, generally single-pointed, crotchets, 55–95 μm long (occasionally such a seta bifid with minute teeth), alternating with about the same number of long hair setae, 200–250 μm long; postclitellar dorsal bundles similar to anterior ones, but setal number and length generally not as great; anterior ventral bundles with two to four bifid setae (Fig. 2A), 65–80 μm long, with very slender, thin and almost parallel teeth, upper tooth tending to be longer than lower; postclitellar ventral bundles with two to three setae, similar to anterior ventrals or sharply single-pointed. Ventral setae of XI, and sometimes

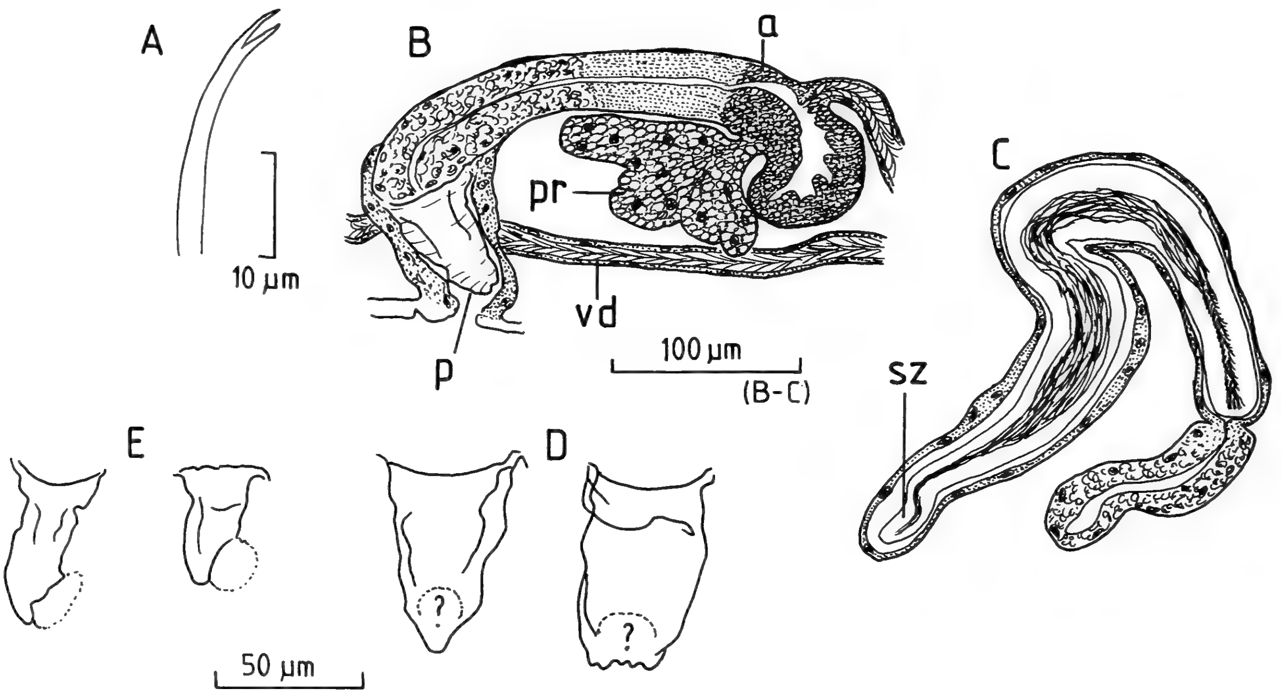

Fig. 2. A–D, *Tubificoides paracrinitus,* n. sp.: A, Ventral anterior seta; B, Male genitalia; C, Spermatheca; D, Penis sheaths; E, *Tubificoides crinitus* Erséus, penis sheaths. Abbreviations: *a* atrium; *p* penis; *pr* prostate gland; *sz* spermatozeugma; *vd* vas deferens.

of X, absent. Spermathecal pores in line with (and near) ventral setae (if present) in middle of X; male pores in line with ventral setae slightly posterior to middle of XI.

Pharyngeal glands in IV–V. Esophagus somewhat enlarged in IX. Male genitalia (Fig. 2B) paired; vas deferens 14–18 μm wide, thin-walled and ciliated, at least about three times longer than atrium, entering latter subapically. Atrium cylindrical, up to about 290 μm long, 33–52 μm wide, histologically tripartite, with up to about 2 μm thick lining of muscles; ental part of atrium more heavily granulated than remaining part; prostate gland lobed, attached to atrium opposite to entrance of vas deferens. Penis (Fig. 2D) with conical, thimble-shaped penis sheath, 70–90 μm long, basally 40–47 μm wide, ectally 27–35 μm wide, with indistinct, terminal or somewhat subterminal(?) opening. Spermathecae (Fig. 2C) with ducts 130–210 μm long, 35–50 μm wide, somewhat glandular and with a hollow ectal swelling; ampullae and spermatozeugmata slender in postcopulatory specimens; sperm trap present(?).

Remarks. — *Tubificoides paracrinitus* is closely related to *T. crinitus* Erséus, 1989, which is simultaneously described from non-seep areas in the same part of the Gulf of Mexico (Erséus 1989b), but it differs from the latter in several respects: (1) it is distinctly larger (0.25–0.27 mm wide at segment XI, as opposed to 0.13–0.22 mm for *crinitus*; length of latter unknown); (2) it has discrete body wall papillae in postclitellar segments (*crinitus* has fine particles scattered over postclitellar segments, but no papillae are formed); (3) it has up to six crotchets and about the same number of hairs in the dorsal bundles (setae only half as many in *crinitus*); (4) occasionally its dorsal crotchets are bifid (well visible in segment V of holotype)(all dorsal crotchets of *crinitus* hair-like and single-pointed); (5) its penis sheaths (Fig. 2D) appear to have smaller and not as lateral openings, as those of the sheaths of *crinitus* (Fig. 2E, shown here for comparison); and (6) its much more slender spermathecae (Fig. 2C) (the spermathecal ampullae of *crinitus* are small and oval). Some of these differences could perhaps, per se, be regarded as intraspecific rather than interspecific, but taken together

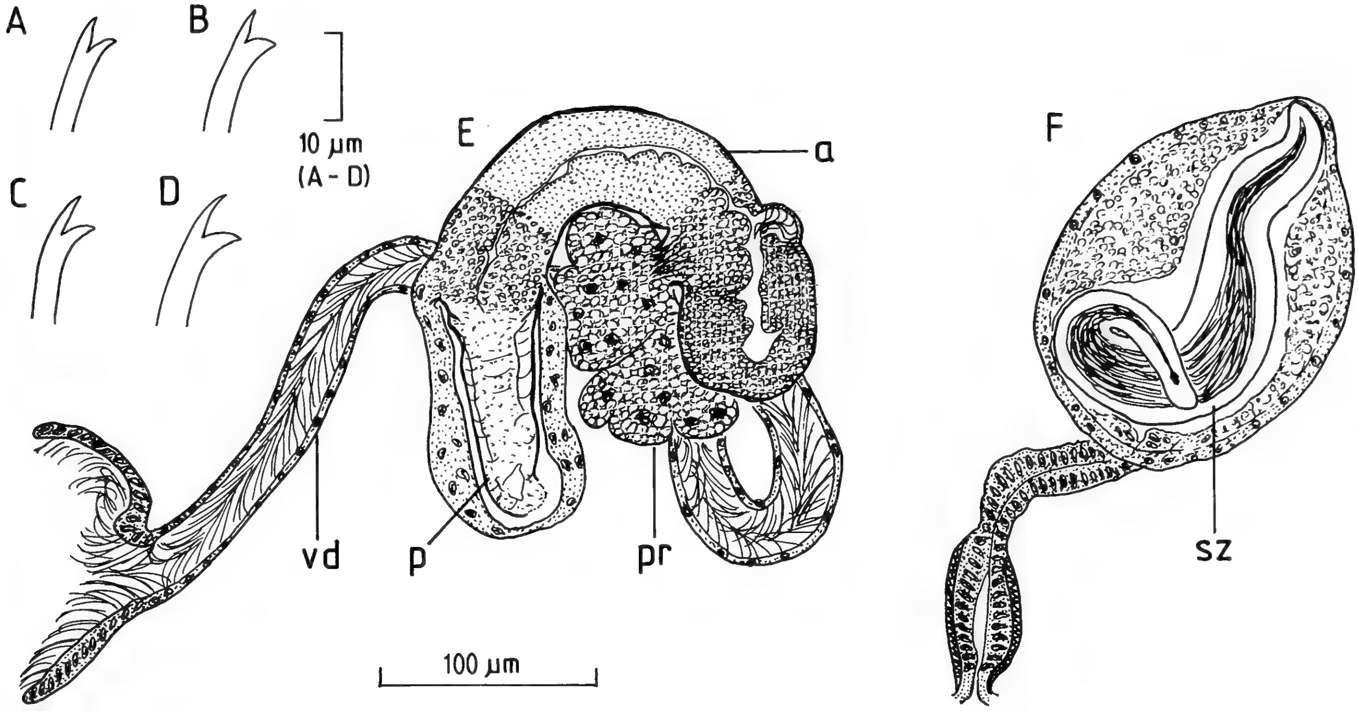

Fig. 3. *Tubificoides pequegnatae,* n. sp.: A, Anterior dorsal bifid seta; B, Posterior dorsal bifid seta; C, Anterior ventral seta; D, Posterior ventral seta; E, Male genitalia; F, Spermatheca. Abbreviations as for Fig. 2.

they certainly indicate that the two forms are separate species.

Distribution and habitat.—Known only from the Gulf of Mexico. Upper continental slope, 540–582 m depth.

Tubificoides pequegnatae, new species
Fig. 3

Holotype.—USNM 119896, whole-mounted specimen from 27°46′56″N, 91°30′20″W, 540.1 m (28 Sep 1986), in area of vestimentiferan growth.

Paratypes.—USNM 119897–119900, four whole-mounted specimens (three of which sexually immature) from type locality.

Etymology.—Named for Dr. Linda H. Pequegnat, who very kindly provided the present material.

Description.—Length of holotype 3.5 mm, 13+ segments (posterior end partially regenerating); sexually mature paratype 2.6 mm, 17 segments, but incomplete. Width at XI in whole-mounted, compressed specimens, 0.32–0.46 mm. Prostomium rounded, somewhat broadly triangular. Body wall naked anteriorly, but coated with fine particles with a tendency to form papillae in postclitellar segments. Clitellum poorly developed. Anterior dorsal bundles with (one) two to three bifid setae, 45–75 µm long, upper slightly longer than lower (Fig. 3A), and (one) two to three hair setae, 115–140 µm long; postclitellar dorsal bundles generally with two bifid setae, upper tooth longer and thinner than lower (Fig. 3B), and occasionally in a few segments immediately posterior to clitellum one hair seta may be present; anterior ventral bundles with three to four bifid setae, 60–75 µm long, upper tooth tending to be longer and thinner than lower (Fig. 3C); postclitellar ventral bundles with two setae (Fig. 3D), similar to anterior ventrals. Ventral setae of X and XI absent. Spermathecal and male pores in line with ventral setae in middle of X and XI, respectively.

Pharyngeal glands in IV–VI. Male genitalia (Fig. 3E) paired; vas deferens about 20 µm wide, thin-walled and ciliated, at least three times longer than atrium, entering latter subapically. Atrium cylindrical, up to about 235 µm long, histologically tripartite, with up to 2 µm thick lining of muscles, ental part of atrium more heavily granulated than remaining part, about 70 μm wide, middle part about 40 μm wide. Prostate gland lobed, attached to atrium opposite to entrance of vas deferens; penis with elongate, funnel-shaped sheath, 75–105 μm long, basally 37 μm wide, with somewhat subterminal opening. Spermathecae (Fig. 3F) with ducts 130 μm long, 20–25 μm wide, ectal region slightly bulbous with a thickened muscular covering; ampullae ovoid, 180–190 μm long, 135–150 μm wide; spermatozeugmata long and slender; sperm trap not seen.

Remarks.—This species is similar to the Northeast Pacific *T. bakeri* Brinkhurst, 1985 with regard to its setal distribution; no other described species in the genus with hairs and bifid setae anteriorly lacks the hair setae in the posterior segments. *Tubificoides bakeri* has a slightly greater number of anterior dorsal setae (up to four bifids, plus as many hairs) than *T. pequegnatae,* and its atria are distinctly smaller than those of the new species, but the most important difference between the two species is the shape of the penis sheaths: the penis of *T. bakeri* has a bulbous tip (Brinkhurst 1985:fig. 7B), whereas the penis of the new species continuously tapers ectally (see Fig. 3E).

Discussion

Seven species of Tubificidae were previously recorded from continental slope depths (about 300 m and deeper) in the northern Gulf of Mexico (Erséus 1988, 1989a, b): *Phallodrilus constrictus* Erséus, *P. grasslei* Erséus, *P. vescus* Erséus, *Bathydrilus connexus* Erséus, *B. longiatriatus* Erséus, *Limnodriloides monothecus* Cook and *Tubificoides crinitus* Erséus. The samples from the "Bush Hill" hydrocarbon seeps yielded three separate species, which is noteworthy considering that the area is located in the same part of the Gulf. It thus seems possible that the three new species, or at least some of them, are endemic to these hydrocarbon seep situations. The extensive bacterial mats (often containing separate phase oil lying between them) probably provides a rich food supply to the associated macrofauna (see Brooks et al. 1987), including these (possibly specialized) tubificids.

Acknowledgments

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EULIMNADIA OVILUNATA AND *E. OVISIMILIS*, NEW SPECIES OF CLAM SHRIMPS (CRUSTACEA, BRANCHIOPODA, SPINICAUDATA) FROM SOUTH AMERICA

Joel W. Martin and Denton Belk

Abstract.—Two new species of the clam shrimp genus *Eulimnadia* are described from South America. *Eulimnadia ovilunata,* a species with spherical eggs bearing circular crater-like depressions, is described from Argentina, and *Eulimnadia ovisimilis,* a species with stout cylindrical eggs that closely resemble those of the North American species *E. texana* (Packard), is described from Paraguay.

Species of the clam shrimp genus *Eulimnadia* Packard (sometimes considered synonymous with *Limnadia*; see Webb & Bell 1979) in North, Central, and South America were the subject of two recent reviews by Belk (1989) and Martin (1989). Although many traditionally employed characters were shown by those authors to be variable and unreliable, an additional character, morphology of the external egg shell, appears to be conservative and species-specific. In his comparison of described Central and South American species, Martin (1989) examined two South America forms that did not conform to any known species. Those species, described from samples in the collections of Denton Belk in San Antonio, Texas, were referred to by Martin as *Eulimnadia* sp. A (DB 305) and *Eulimnadia* sp. B (DB 632). In this paper we describe the two new species.

Materials and Methods

Illustrations were made from ethanol-preserved specimens with a Wild M-5APO stereoscope with camera lucida. All specimens are catalogued in the Natural History Museum of Los Angeles County, abbreviated LACM. The abbreviation DB refers to the cataloging system of the private collection of the junior author in San Antonio, Texas; lots from that private collection formed the basis for this report.

The highway designations in Catamarca Province, Argentina, changed between the time Arthur Hulse made clam shrimp collections in 1973–1974 and today. We cite the current nomenclature according to the 14 April 1986 map published by Automovil Club Argentino in addition to including the location information originally supplied by Dr. Hulse (in parentheses).

Eulimnadia ovilunata, new species
Figs. 1, 3A–C

Eulimnadia sp. A.—Martin, 1989, fig. 5d (eggs).

Material.—DB 303, paratypes, LACM 74-107.1, 3 males, 45 females (22 ovigerous), Argentina, Catamarca Province, highway 46 W of Andalgalá in flood plain of Río Amanao (formerly Route 62, km 1508, at time of collection), 4 Mar 1974, coll. A. Hulse; DB 304, paratypes, LACM 74-108.1, 11 females (1 ovigerous), Argentina, Catamarca Province, highway 46 S of Andalgalá (formerly Route 1, km 104, at time of collection), 8 Mar 1974, coll. A. Hulse; DB 305, holotype female (ovigerous), LACM 73-180.1; paratypes, LACM 73-180.2, 19 fe-

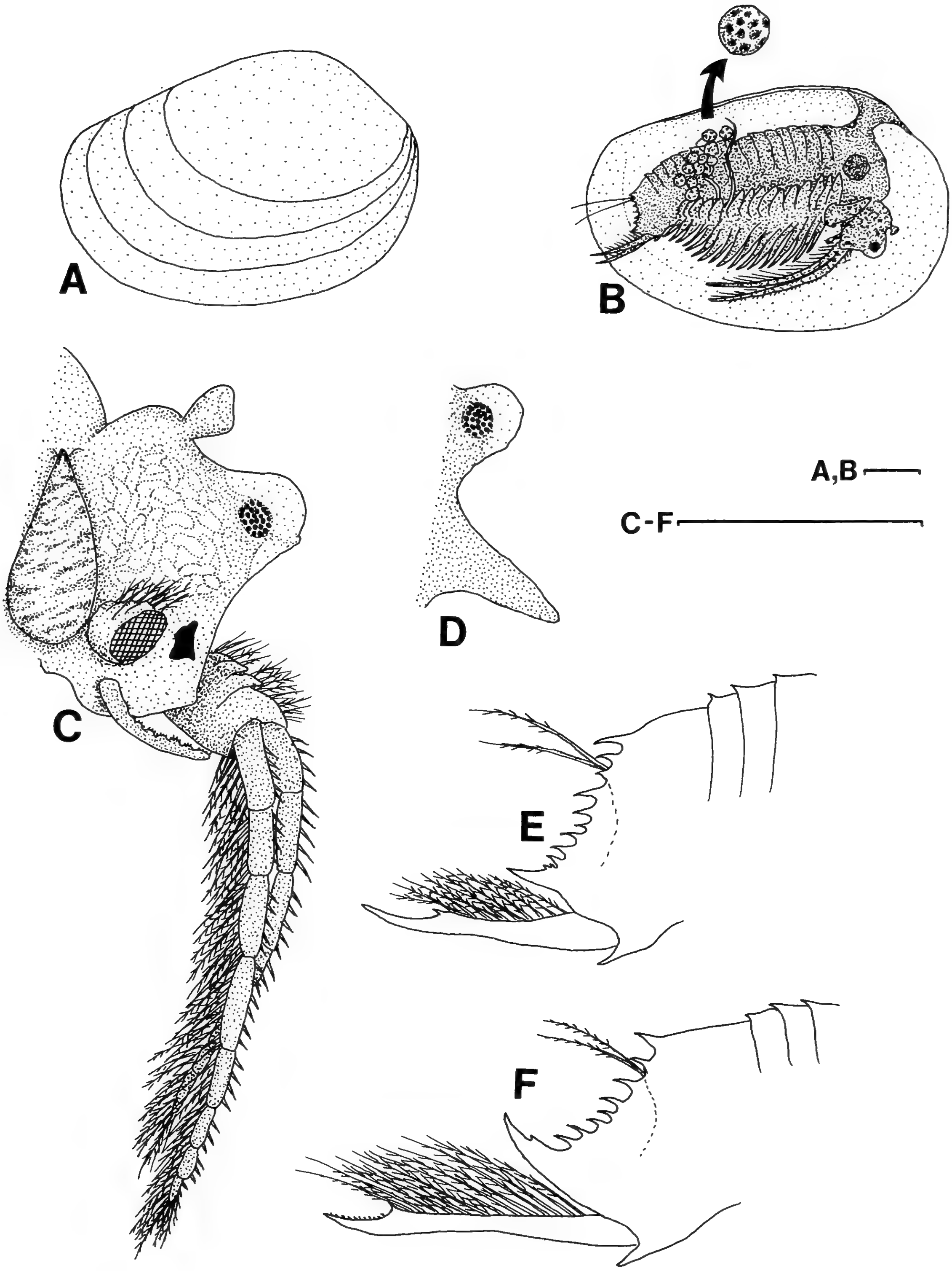

Fig. 1. *Eulimnadia ovilunata*: A, Right valve of holotype female; B, Holotype female, right valve removed, with egg enlarged above; C, Frontal region of holotype female; D, Rostrum and eye of one of three poorly preserved males; E, Caudal region of holotype female; F, Caudal region of male. Scale bars indicate 1.0 mm.

males (15 ovigerous), Argentina, Catamarca Province, highway 46 S of Andalgalá (formerly Route 1, km 45, at time of collection), 30 Dec 1973, coll. A. Hulse, 1 female destroyed in SEM preparation (Fig. 3).

Measurements.—Male carapace 5.5 to 6.0 mm length, 3.5 to 4.1 mm height (but see Remarks below) (n = 3; DB 303, no males in other collections). Female carapace 5.1 to 6.8 mm length, 3.3 to 4.7 mm height (n

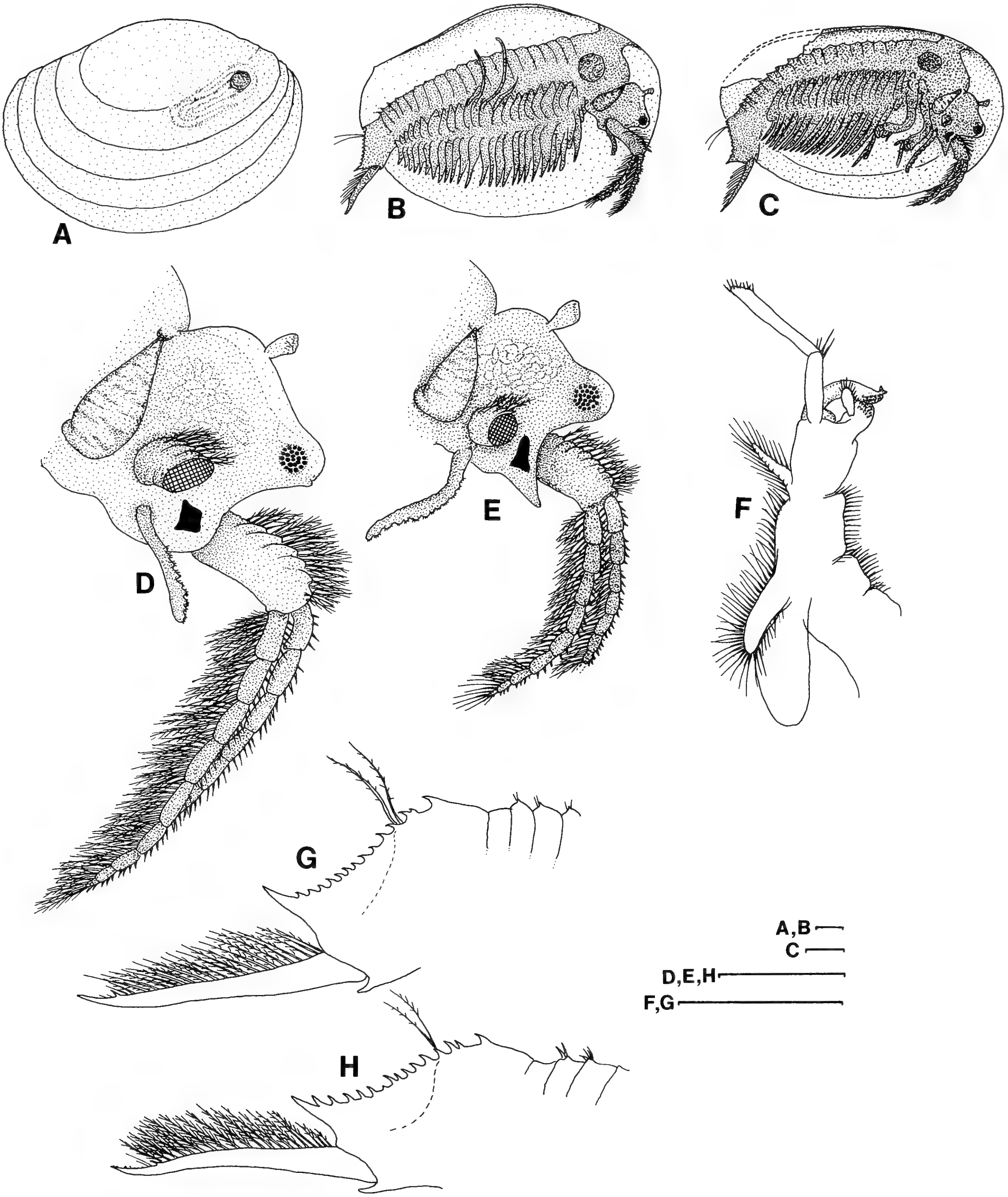

Fig. 2. *Eulimnadia ovisimilis*: A, Carapace (right valve) of holotype female; B, Holotype female with right valve removed; C, Allotype male with right valve removed; D, Head region of holotype female; E, Head region of allotype male; F, Second male clasper of allotype male; G, Caudal region of allotype male; H, Caudal region of holotype female. Scale bars indicate 1.0 mm.

= 76, DB 303, DB 304, DB 305; smallest and largest females both ovigerous).

Carapace.—Female carapace (Fig. 1A, B) broadly oval, with hinge border domed and with three or four lines of growth. Male carapaces all shriveled; condition indeterminate (see below).

Head region.—Female (Fig. 1C) with broadly triangular rostrum; male (Fig. 1D) with very prominent acute rostrum.

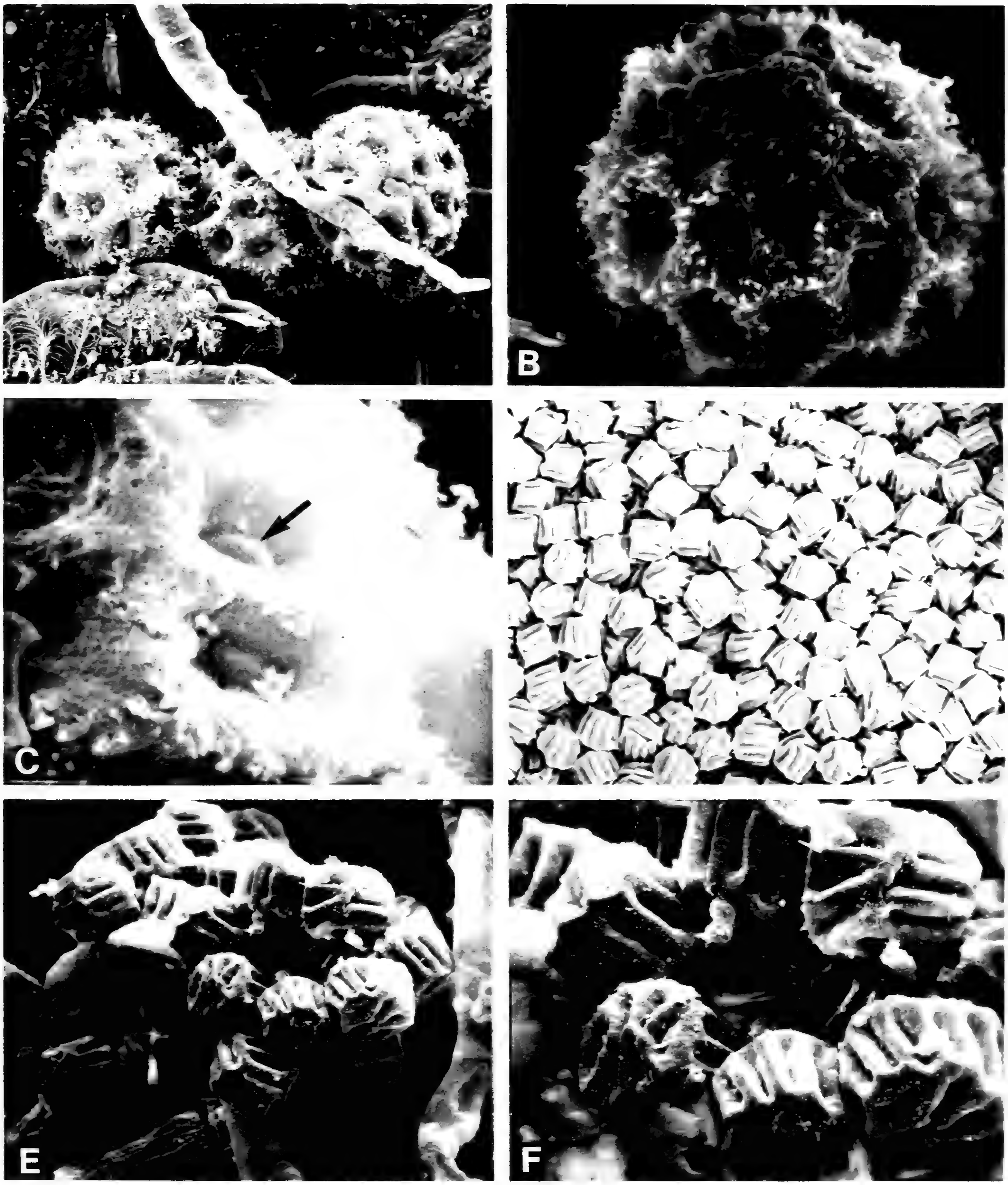

Fig. 3. Scanning electron micrographs of eggs of *Eulimnadia ovilunata* (A–C) and *E. ovisimilis* (D–F): A, Eggs of *E. ovilunata* (paratype) from Catamarca, Argentina (DB 305), ×200; B, Single egg of *E. ovilunata* (from same female as in A), ×520; C, Higher magnification of crater-like depression of egg in B showing mound at bottom of depression (arrow), ×1,180; D, Eggs of *E. ovisimilis* (paratype) from Paraguay (DB 632), ×75; E, Cluster of eggs of *E. ovisimilis* on epipod of female, ×120; F, Higher magnification of eggs shown in E showing nature of end pieces, ×250.

Antennae.—First antennae pseudosegmented with aesthetascs on anterior border of each lobe. Second antennae natatory, with spines on dorsal border and plumose setae on ventral border of each segment; number of segments varies from seven to nine.

Male thoracopods.—Not examined (see below).

Caudal region.—Female (Fig. 1E) and male (Fig. 1F) caudal regions similar, with 8 to 10 stout downward curved spines on posterior borders and with telsonal filaments arising from between second and third such spines.

Eggs.—Spherical, with oval or circular depressions that appear fringed with small fingerlike projections of the shell or tertiary envelope, each depression with a slightly convex and relatively smooth floor (Figs. 1B, 3A–C).

Type locality.—Argentina, Catamarca, highway 46, 45 km S of Andalgalá.

Range.—Known from three localities in Catamarca, Argentina.

Etymology.—From the Latin "luna" (moon) and "ova" (egg), because the depressions on the eggs are reminiscent of craters on the lunar surface.

Remarks.—*Eulimnadia ovilunata* does not differ appreciably from many other species of the genus except by virtue of the egg morphology. Of the South American species described or reviewed by Martin (1989), only the egg of *E. brasiliensis* Sars is spherical. However, the *E. brasiliensis* egg lacks the minute projections fringing each indentation, and the indentations do not appear as regularly formed and do not bear the clearly defined oval "floor" of the crater (compare Martin's (1989) fig. 4c to his fig. 5d and to Fig. 3A, this paper). The North American species *Eulimnadia diversa* Mattox, *E. agassizii* (Packard), and *E. antlei* (Mackin) also have spherical eggs, but the eggs of all three of these species clearly differ from *E. lunaova* eggs under high magnification (see Belk 1989). The eggs of *Eulimnadia antillarum* (Baird), a species that occurs in North and South America, remain undescribed, but the caudal region of that species is nearly devoid of spines (see Martin 1989:fig. 5A), whereas the caudal region in *E. ovilunata* bears relatively large, well developed spines in both sexes (Fig. 1E, F).

The only males in the series are in very poor condition, apparently having completely dried out at some time in the past. Structures traditionally described for males could not be ascertained, and the illustration of the male rostral region (Fig. 1D) should be verified when males in good condition are collected. Because of the condition of the males no allotype was designated among the three male paratype specimens in DB 303.

Eulimnadia ovisimilis, new species
Figs. 2, 3D–F

Eulimnadia sp. B.—Martin, 1989, fig. 5e–g (eggs).

Material.—DB 632, holotype female (ovigerous), LACM 84-204.1; allotype male, LACM 84-204.2; paratypes (2 males, 48 females (21 of which are ovigerous)), LACM 84-204.3, Paraguay, Chaco Departamento, Parque Nacional Defensores del Chaco, Tribo Nuevo, "encontrado en regiónes bajas de laguna recién inundada," from shallow regions with submerged grass about one week after heavy rains filled a formerly dry pond-marsh (Terry Bonace, personal letter to D. Belk), 23 Nov 1984, coll. T. Bonace and D. Drenner.

Measurements.—Male carapace 6.9 to 7.5 mm length, 4.5 to 4.7 mm height. Females (including ovigerous females) 6.0 to 10.0 mm length, 4.2 to 6.9 mm height.

Carapace.—Female carapace (Fig. 2A, B) broadly oval, distinctly elevated along dorsal border, with four lines of growth. Male carapace (Fig. 2C) usually smaller, oval but not elevated along dorsal border, instead somewhat flattened along hinge line, with two or three lines of growth.

Head region.—Female (Fig. 2D) with very short bluntly rounded rostrum; male (Fig. 2E) with short but acute rostrum.

Antennae.—Similar to that described for *E. ovilunata* (and many other members of the genus); second antennae with eight or nine segments.

Male thoracopods.—Typical for the genus, with long 2-segmented palp, stout distal spines on clasper border, and small cup-like projection on distal border of clasper finger (Fig. 2F).

Caudal region.—Similar in males (Fig. 2G) and females (Fig. 2H), with 13 to 17 stout caudal spines and with telsonal filaments arising from about level of fourth posterior spine.

Eggs.—Stout and cylindrical, with parallel grooves separating rounded ridges along cylinder axis and with perpendicular grooves on end pieces (Fig. 3D–F; see also Martin 1989, fig. 5e–g).

Type locality.—Paraguay, Chaco Departamento, Parque Nacional Defensores del Chaco, Tribo Nuevo, "encontrado en regiónes bajas de laguna recién inundada," shallow region with submerged grass.

Range.—Known only from the type locality.

Etymology.—The name refers to the marked similarity that eggs of this species bear to eggs of the North American species *E. texana* (see Belk 1989).

Remarks.—The eggs of *Eulimnadia ovisimilis* are virtually identical to those of *E. texana,* a predominantly North American species that has been reported, probably mistakenly, as far south as Sao Paulo, Brazil (Lutz 1929, Daday 1926). This is disturbing in light of our recent findings that egg morphology is often species-specific in the Limnadiidae and is in any case a more conservative taxonomic character than any previously employed feature. Indeed, we at first thought that we had encountered a southern hemisphere population of *E. texana* rather than an undescribed form. However, there are several salient differences between the two species. In *E. texana* males and females have a similar rostral morphology. In contrast, sexual dimorphism is marked in *E. ovisimilis.* In females of *E. ovisimilis* the rostrum is rounded and slightly protruding, whereas in males the rostrum is attenuated and sharply produced (see Fig. 2D, E). Although there is known to be variation in rostral morphology in *E. texana,* there is never sexual dimorphism as marked as is seen in *E. ovisimilis* (Sissom 1971, Belk 1989). Additionally, the eggs of *E. ovisimilis* appear less domed on the end pieces than are eggs of *E. texana.*

Discussion

Morphology of the external egg shell has been shown to be a useful and reliable character in identifying species of the genus *Eulimnadia* (Belk 1989). Some caution is advised when consulting previous published accounts of egg morphology where scanning electron microscopy was not used. Specifically, some of the illustrations or verbal accounts given by Daday (1926) were shown by Belk (1989) to be erroneous or lacking in sufficient detail to be of taxonomic value, perhaps a result of limitations of the microscopy available at that time. Even when SEM is applied, however, there may be cases where egg morphology will fail to distinguish between two otherwise recognizable species. This was pointed out by Mura (1986) for distinct species of anostracans that have identical egg morphologies, and the present paper demonstrates that this scenario also occurs in some species of clam shrimp (Spinicaudata only; the Laevicaudata do not have sculptured eggs; Martin & Belk 1988). This need for caution was noted by Belk (1989) in anticipation of this sort of problem. We emphasize again the need for using SEM on branchiopod egg morphology, but advise against using egg morphology to the exclusion of other characters.

Finally, as mentioned briefly by Belk (1989) and Martin (1989), the present status of the genera *Limnadia* Brongniart and *Eulimnadia* Packard is unclear. Most morphological characters previously used for separating the two genera are variable, and there is some overlap, leading several workers to suggest that the two genera should be synonymized (Webb & Bell 1979). However, there are at least two characters that serve to separate the two genera for species in the Americas. First, the well developed spine on the posteroventral border of the caudal somite is always easily discerned in *Eulimnadia,* whereas in the only species of *Limnadia* known from the Americas (*L. lenticularis*) this spine is absent (although a small lobe is present in the same location). Webb & Bell (1979:fig. 1) show a morphological gradation from one state to the other based on drawings in existing literature, and suggest that this character is therefore unreliable. Second, the telsonal filaments arise from between the paired spinose posterocaudal borders in all American *Eulimnadia,* whereas in *Limnadia lenticularis* the filaments arise from a location anterodorsal to the point where these borders become fused. We will address these two characters and the status of *Eulimnadia* vs. *Limnadia* in a future paper.

Acknowledgments

Much of this paper was written or planned during a brief visit by JWM to San Antonio, Texas, during which time the hospitality and assistance of Mary Shug Belk was greatly appreciated by both authors. Captain J. Trent Collier, U.S. Air Force, assisted in the collection of specimens used later for comparative work and provided useful discussion. We thank Arthur C. Hulse and Terry Bonace for collecting and giving to Denton Belk the specimens used in these descriptions. This work was supported by the National Science Foundation, grant no. BSR-8615018 to J. W. Martin and L. G. Abele.

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DANTYA FEROX, A NEW SPECIES OF MYODOCOPID OSTRACODE FROM NIUE, CENTRAL SOUTH PACIFIC (CRUSTACEA: OSTRACODA: SARSIELLIDAE)

Louis S. Kornicker and Thomas M. Iliffe

Abstract.—Dantya ferox, a new species of myodocopid ostracode in the subfamily Dantyinae from a marine cave in the island of Niue, central South Pacific, is described and illustrated. The genus had not been reported previously from the Pacific. A key is presented to the species of *Dantya.*

The genus *Dantya,* proposed in 1978, is now known from five species, but specimens are sparse, with only one species known from more than two specimens (*Dantya benthedi*—50 specimens, *D. magnifica*—2 specimens, and *D. fossula, D. piercei,* and *D. ferox*—1 specimen for each species). The adult male is not known for any of the species, but this is not unusual in the Sarsiellidae, because the ratio of females to males is high; as a consequence systematic discrimination in the family is based mostly on female characters.

The island of Niue is a raised limestone atoll encompassing 259 square km located 386 km east of Vava'u, Tonga, in the central South Pacific Ocean (Fig. 1). A 20 m sea cliff at the inner edge of a narrow reef platform surrounds the island. Inland, a second terrace rises to a central plateau about 60 m above sea level. Faulting during uplift has produced many deep chasms which run parallel to the coastline. Well developed karst relief is present around the margins of the island.

An adult female of a new species, *Dantya ferox,* described herein, was collected inside a cave with direct connection to the sea along the west side of the island. The species is not considered to be a troglobite because of the open connection of the cave to the sea; this conclusion is supported by the species having normal eyes. This is the first report of the genus in the Pacific Ocean; previously, the genus was known only from the Caribbean Sea (one species) and Indian Ocean (three species).

Sarsiellidae Brady & Norman, 1896

Composition.—The Sarsiellidae include two subfamilies: Sarsiellinae Brady & Norman, 1986, and Dantyinae Kornicker & Cohen, 1978.

Dantyinae Kornicker & Cohen, 1978

Composition.—The Dantyinae include two genera: *Dantya* Kornicker & Cohen, 1978, and *Nealella* Kornicker & Caraion, 1980.

Dantya Kornicker & Cohen, 1978

Type species.—Dantya magnifica Kornicker & Cohen, 1978.

Composition.—The new species described herein increases the number of known species of the genus to five: *D. magnifica* Kornicker & Cohen, 1978, *D. benthedi* Kornicker, 1983, *D. piercei* Kornicker, 1983, *D. fossula* Kornicker, 1983, and *D. ferox,* new species.

Distribution.—D. magnifica is known only from a coral reef fringing Carrie Bow Cay, Belize, Caribbean Sea, where it was collected at a depth of 20 m. *D. fossula* and *D.*

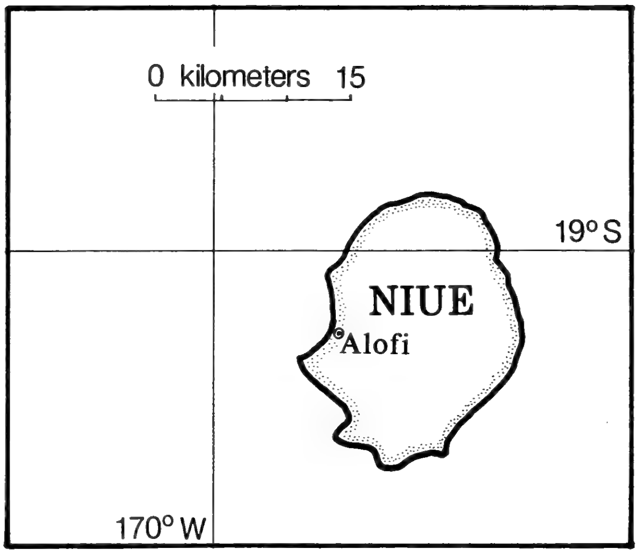


Fig. 1. Map showing location of the island of Niue, central South Pacific Ocean. Cave from which *Dantya ferox* was collected is near Alofi.

benthedi were collected in the Mozambique Channel, Indian Ocean, at depths of 24 m and 250–550 m, respectively. *D. piercei* was also collected in the Indian Ocean, on the continental shelf east of the Somali Republic at a depth of 60–70 m. The new species, *D. ferox,* was collected at a depth of 2 m in a sea cave on the island of Niue, central South Pacific Ocean.

Key to the Species of *Dantya* (females)

1. Ventral margin of rostrum forming right angle with anterior margin of valve ventral to rostrum 2
- Ventral margin of rostrum forming acute angle with anterior margin of valve ventral to rostrum 3
2. Surface of valves with numerous minute knob-like processes; dorsal margin of second joint of first antenna with one bristle ... *D. magnifica*
- Surface of valves without knob-like processes; dorsal margin of second joint of first antenna without bristle .... *D. ferox,* new species
3. Longest ventral claw of first endopodial joint of mandible with three stout teeth, without slender teeth and spines .... *D. benthedi*
- Longest ventral claw of first endopodial joint of mandible with slender teeth and spines and without three stout teeth 4
4. Second endopodial joint of mandible with five claws .... *D. piercei*
- Second endopodial joint of mandible with two claws .... *D. fossula*

Dantya ferox, new species
Figs. 2–6

Etymology.—From the Latin *ferox* (wild, spirited, fierce) in reference to the name Savage Island by which the island of Niue is also known.

Holotype.—USNM 193645, adult female on slide and in alcohol, unique specimen.

Type locality.—PWD (Public Works Department) Cave (Stn. 88-012), Alofi, leg. T. M. Iliffe, 23 Feb 1988; unique specimen collected in a plankton net from gravel bottom of cave in 2 m depth and 5 m inside the cave from the sea.

Description of cave.—PWD Cave is a sea cave located on the west coast of Niue and behind the Public Works Department depot at Alofi. It is reached by a tourist footpath south of the depot which leads to the coast. The cave is at the back of a small sheltered bay. It consists of a sea water filled fissure approximately 10 m in length with a small dry section at the inner end. Water depth in the cave is 2 m with a gravel bottom. The water temperature was 29°C on 23 Feb 1988. The walls of the cave were relatively barren despite the direct connection with the sea, and had only a few small sponges and other encrusting organisms. A sea snake was observed in the rear of the cave. Amphipods, tanaidaceans and isopods were also collected.

Description of adult female (Figs. 2–6).—Carapace elongate with prominent rostrum with pointed tip, and elongate caudal process with truncate tip (Figs. 2, 3a).

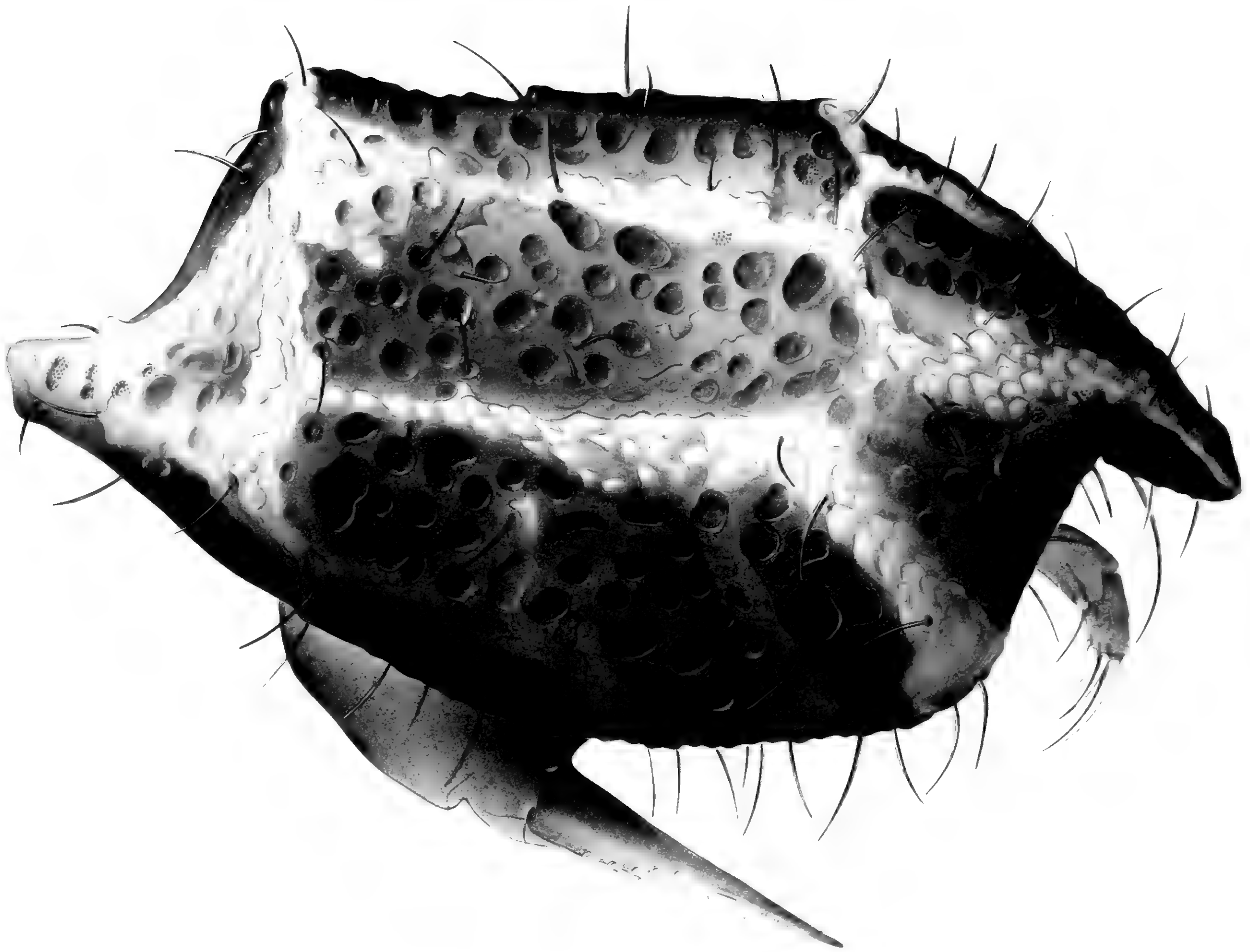


Fig. 2. *Dantya ferox,* holotype, adult female, USNM 193645: Lateral view of complete specimen from right side, length 0.99 mm. All over tone for shape, contour and lighting done with airbrush.

Ornamentation: Surface with numerous oval fossae with crenulate or papillate edges and papillate bottoms, and two low horizontal ribs formed of platelets having crenulate posterior edges (Figs. 2, 3b); platelets closer together at anterior and posterior ends of ribs than at midlength (Fig. 2); surface of platelets with minute pores or papillae (difficult to resolve) (Fig. 3b). Upper rib with anterior end at tip of rostrum and posterior end at posterodorsal corner of valve; lower rib passing over lower half of central adductor muscle attachments, with anterior end at anteroventral corner of valve and posterior end at vertical ridge anterior to caudal process; upper and lower ribs weakly connected by low vertical rib at about one-fourth length of valve from anterior end (Fig. 2); vertical rib extends dorsally and branches near dorsal edge of valve.

Carapace bristles: Outer surface with widely scattered medium and long bare bristles, some with broad base, most with bases in shallow round fossae (Fig. 2). Inner side of rostrum with two bristles forming row near ventral margin (Fig. 3c); inner side of anteroventral margin with about 12 bristles forming row close to valve edge and five bristles forming distal row closer to edge (Fig. 3d); inner side of ventral margin with eight bristles forming row.

Infold: Anterior edge of infold at posterior end of rostrum with three spinous bristles forming verticle row, and one shorter bare bristle near inner corner of incisur (Fig. 3c). Broad anteroventral infold with three parallel ridges, one small bare bristle at midwidth ventral to rostrum, and three similar bristles near outer edge at anteroventral curvature of valve (Fig. 3d). Infold of caudal

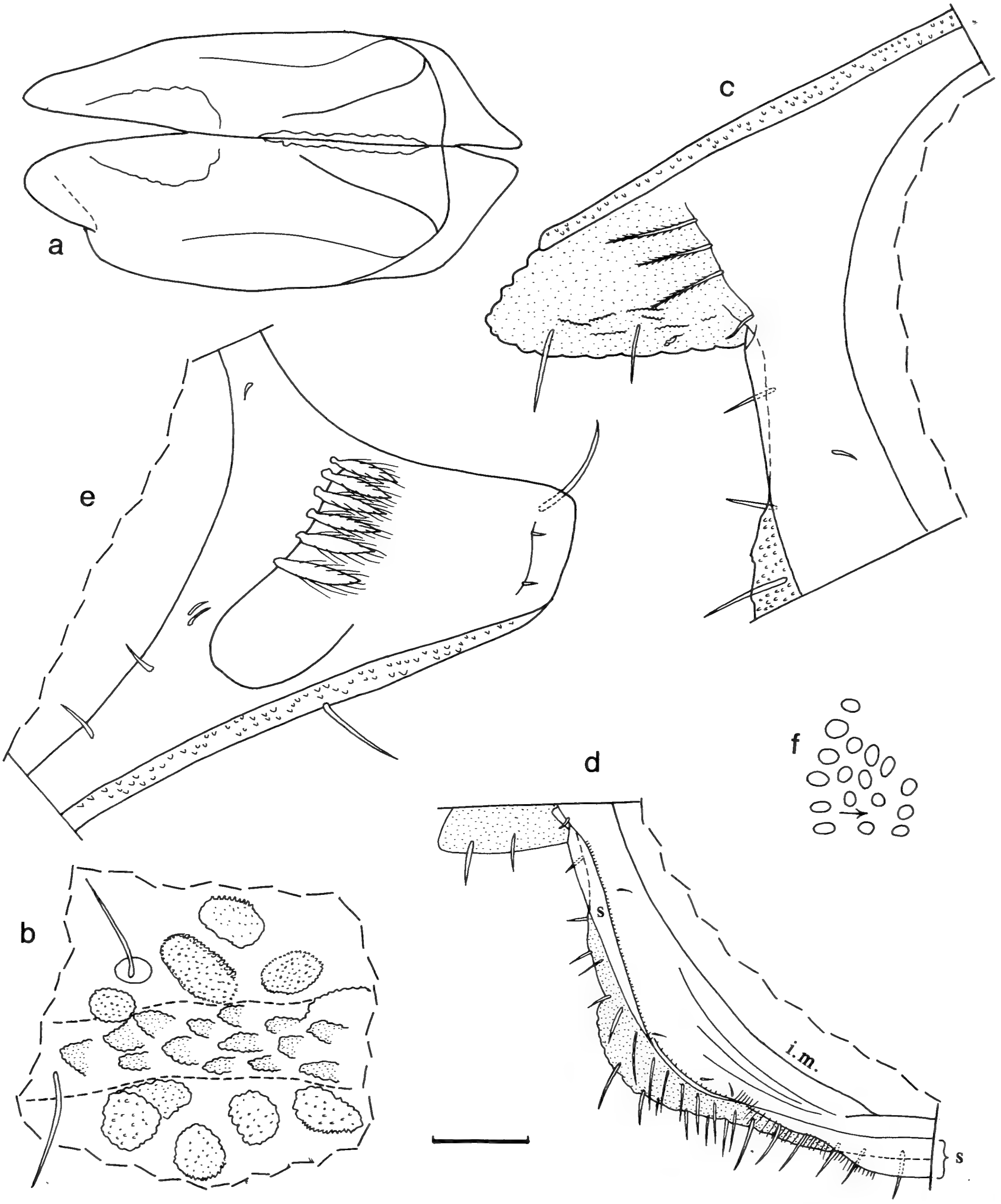


Fig. 3. *Dantya ferox,* holotype, adult female, USNM 193645: a, Dorsal view of complete specimen, anterior to left, length 0.99 mm (specimen slightly oblique and with valves open slightly); b, Detail of surface of right valve at midlength of lower rib; c, Inside view of anterior of right valve; d, Inside view of anteroventral margin of right valve; e, Inside view of caudal process of right valve; f, Outside view of central adductor muscle attachments of right valve, anterior to right. Abbreviations: i.m., inner margin of infold; s, selvage. Scale bar represents 0.1 mm for d, and f, and 0.05 mm for b, c, e.

process with four bristles along inner margin, and "pocket" with six or seven flat frond-like bristles forming row along anterior edge of pocket, and two small indistinct spines forming row near posterior edge of caudal process (Fig. 3e).

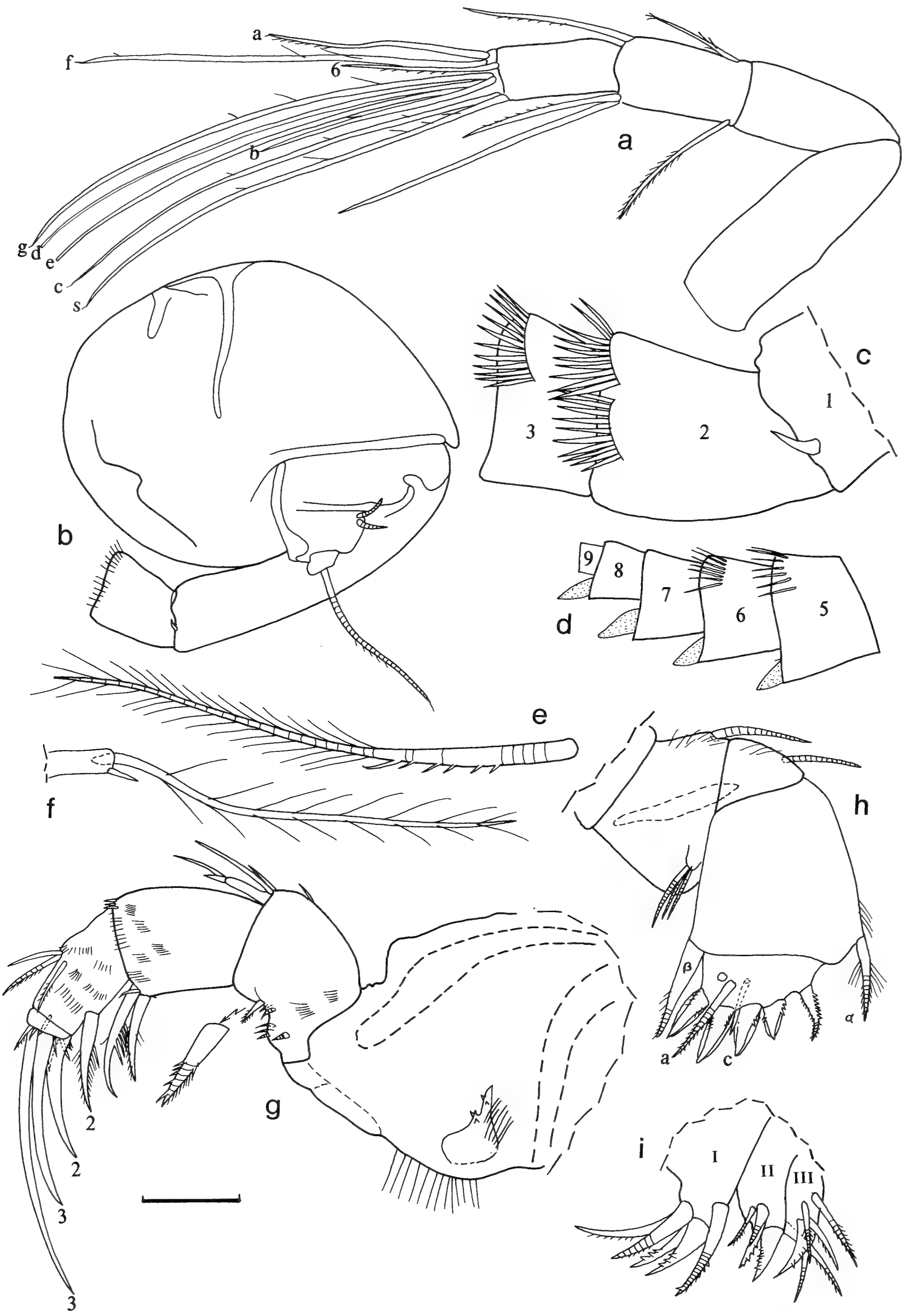
Selvage (Fig. 3d): Lamellar prolongation of selvage with anterior end near ventral spinous bristle of rostral infold and posterior end at ventral end of caudal process; prolongation between inner end of incisur and anteroventral corner of valve with short marginal spines; short section of prolongation posterior to anteroventral corner with long streamers along margin; posterior to that section prolongation broader, either bare or with minute marginal spines; prolongation narrow and bare along ventral margin of caudal process and absent along posterior edge (not shown); dorsal edge of rostrum and caudal process with narrow prolongation (not shown).

Central adductor muscle attachments (Fig. 3f): Consisting of about 17 discrete oval attachments.

Carapace size: Holotype: length 0.99 mm, height 0.58 mm.

First antenna (Fig. 4a): First joint bare. Second joint with minute medial spines forming row in distal dorsal corner. Third and fourth joints and also fifth and sixth joints fused but each joint identified by distribution of bristles. Third joint with two bristles: dorsal bristle with long proximal hairs and few minute spines at tip; ventral bristle longer and with short marginal spines. Fourth joint with three bristles: single dorsal bristle with few indistinct short spines; shorter of two ventral bristles medial and with indistinct short spines; longer of ventral bristles lateral, bare. Ventral bristle of long fifth joint with five small filaments and minute process at tip. Sixth joint with spinous medial bristle longer than fused fifth and sixth joints. Seventh joint: a-bristle longer and stouter than bristle of sixth joint, with few indistinct short spines; b-bristle slightly longer than a-bristle, with short distal filament and minute process at tip; c-bristle about same length as bristle of fifth joint, with three small marginal filaments and minute process at tip. Eighth joint: d- and e-bristles same length as c-bristle, bare with blunt tips; f-bristle shorter than c-bristle, with two short proximal filaments, one minute subterminal filament or spine, and minute process at tip; g-bristle same length as c-bristle, with two short proximal filaments, one minute filament or spine near midlength, and minute process at tip. All bristles ringed (rings not shown).

Second antenna: Protopodite bare (Fig. 4b). Endopodite two-jointed (Fig. 4b): first joint with two small ringed proximal anterior bristles; second joint small, with long ringed bristle with short marginal spines. Exopodite (left limb): first joint with small recurved medial bristle near midwidth of distal margin (Fig. 4c); bristles of joints 2–8 long, with six proximal ventral spines (distal spine longest) followed by natatory hairs (Fig. 4e); bristles of joints 4–7 with dorsal hairs proximal to spines; ninth joint small, with two bristles (ventral bristle shorter and slenderer than bristle of eighth joint, with three small proximal ventral spines followed by one longer dorsal spine, then natatory hairs; dorsal bristle of ninth joint short with few small hair-like marginal spines). Joint 2 with spines forming two distal rows (Fig. 4c); joints 3–6 with spines forming one distal row (Fig. 4c, d); spines mostly on medial side but rows curving around dorsal edge of joint resulting in few spines being on lateral side near dorsal margin. Joints 4–8 with basal spines increasing in size on distal joints (spine on eighth joint about twice length of small ninth joint (Fig. 4d). Exopodite of right limb aberrant, with only seven joints: small medial terminal bristle of first joint straight, not bent as on left limb; bristles of joints 2–5 similar to those of left limb; bristle of sixth joint with only three ventral spines and distal part invaginated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into base (Fig. 4f); terminal seventh joint larger than terminal ninth joint of left limb, with two bristles (longest bristle ventral, with three ventral spines and without natatory hairs; dorsal bristle minute, about half length of seventh joint); joints 2–6 with long medial spines forming one to three rows arranged differently than on left limb; joints 2–6 with basal spines. (Exopodial bristles not shown in Fig. 4c, d.)

Mandible (Fig. 4g): Coxale endite with stout terminal spine with two or three smaller marginal spinules, a subterminal spine with two smaller marginal spines, and long slender spines forming two proximal rows; ventral edge of coxale with slender spines forming two or three rows. Basale: medial side near ventral margin with three small ringed bristles (distal stouter and with marginal spines); medial side near proximal margin with two rows of spines; lateral side near ventral margin with row of three minute bare ringed bristles; dorsal margin with short ringed bristle distal to midlength and two terminal ringed bristles (longest reaching midlength of first endopodial joint) (rings on bristles not shown). Exopodite cylindrical, about one-third length of dorsal margin of first endopodial joint; tip with short diaphanous triangular flap and ringed bristle (rings not shown). First endopodial joint: medial side with rows of distal spines; dorsal margin with row of terminal spines (spines stouter than those of medial side); ventral margin with small medial ringed terminal bristle (rings not shown) and two terminal claws (proximal medial claw with slender marginal spines, other stouter and with four or five stout ventral spines at midlength (spines increasing in length and stoutness distally along claw). Second endopodial joint: dorsal margin with three bristles (one bare, two with spines); ventral margin with stout claw (with ventral and dorsal spines) distal to midlength, and stouter terminal claw with few proximal ventral spines; medial surface with slender spines forming rows; lateral surface with small indistinct terminal bristle near midwidth. Third endopodial joint with one short spinous dorsal claw, one small unringed spine-like bristle adjacent to dorsal claw (indistinct and observed only on right limb), two small ringed lateral bristles near ventral margin, two stout bare unequal terminal claws, and one small medial spine just ventral to shortest stout terminal claw (spine could be on claw).

Maxilla (Fig. 4h, i): Coxale with stout dorsal bristle. Endites I, II, and III each with five bristles (Fig. 4i). (Note: in Fig. 4i anterior bristle of endite II is behind endite III making it appear to be on that endite.) Basale with spinous dorsal bristle and distal medial bristle (not shown in Fig. 4h). Exopodite with three terminal ringed spinous bristles (one longer than others). First endopodial joint: alpha-bristle with distal rings, long proximal hairs and short distal spines; beta-bristle stouter than alpha-bristle, ringed only near tip, with short distal hairs; anterior margin and medial surface near anterior margin with long spines (not all shown). Second endopodial joint with

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Fig. 4. *Dantya ferox,* holotype, adult female, USNM 193645: a, Medial view of right first antenna. b–e, Medial views of left second antenna: b, Protopodite, endopodite, and exopodial joints 1 and 2; c, Joints 1–3 of exopodite; d, Joints 5–9 of exopodite; e, Bristle of second exopodial joint; f, Tip of invaginated bristle of sixth joint of exopodite of aberrant right second antenna; g, Medial view of right mandible; h, Lateral view of right maxilla (endites not shown); i, Medial view of endites of right maxilla. Abbreviations: a–g, letters assigned to bristles; s, sensory bristle of fifth joint of first antenna; Arabic numbers, numbers assigned to individual joints; Roman numerals, numbers assigned to endites. Scale bar represents 0.05 mm for a, b, e, g–i, and 0.02 mm for c, d, f.

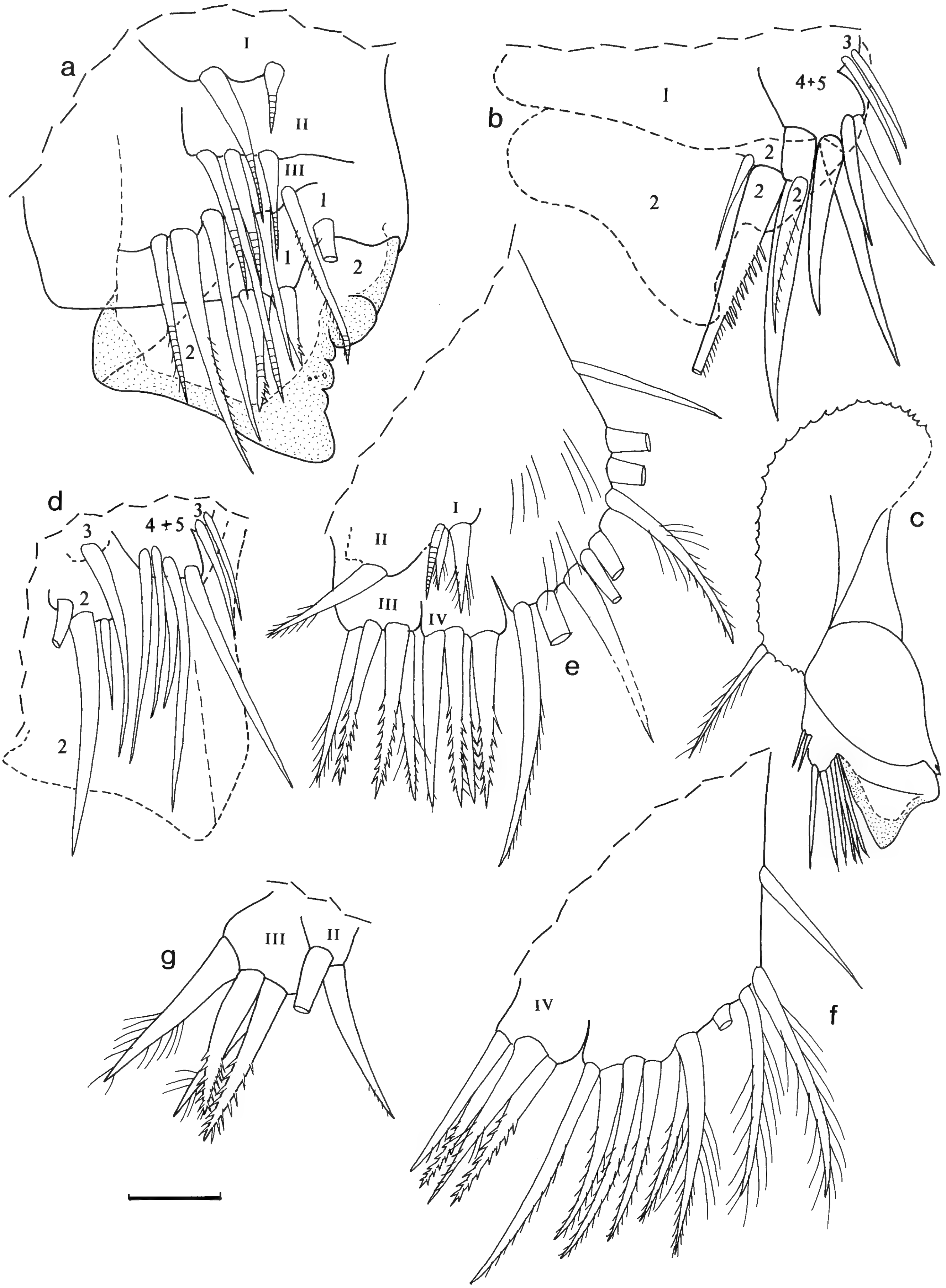

Fig. 5. *Dantya ferox,* holotype, adult female, USNM 193645: a, Anterior view of right fifth limb; b, Posterior bristles of right fifth limb as seen through limb; c, Posterior view of right fifth limb as seen attached to body (only 1 epipodial bristle shown); d, Posterior bristles of exopodial joints 2–5 of left fifth limb as seen through

two spinous lateral a-bristles (one missing on illustrated right limb), one smaller and more slender ringed spinous medial c-bristle, and five terminal bristles: anterior bristle ringed distally and with slender teeth along margins (teeth longer and stouter along unringed part); other bristles stouter, unringed, with teeth along margins proximal to midlength, and with narrow transparent velum along each edge (Fig. 4h). (Note: a dorsal bristle was observed on a coxale when the maxilla was attached to the body, but was absent on each mounted limb; I assume that the bristle was broken off during dissection; a visible empty socket on the right limb supports the assumption.)

Fifth limb (Fig. 5a–d): Epipodite with about 40 bristles (Fig. 5c). Endite I with two bristles; endite II with three bristles; endite III with six bristles (Fig. 5a). Exopodite: first joint: anterior side with two short pectinate bristles at midwidth and one closer to inner edge (Fig. 5a). Second joint: large square tooth with proximal round tooth on inner edge (Fig. 5a); posterior side with three bristles forming row (middle bristle stout pectinate) (Fig. 5b, d) (teeth not shown on middle bristle in Fig. 5d). Third joint with two short bristles on outer lobe and one long bristle on inner lobe (Fig. 5b, d) (bristle of inner lobe could be on first or second joints; bristle observed only on left limb). Fourth and fifth joints fused, with total of five bristles (Fig. 5b, d).

Sixth limb (Fig. 5e–g): Limb partly fragmented during dissection, with four endites. Endite I with three short bristles; endite II with two bristles (one missing in Fig. 5e); endites III and IV each with four bristles. End joint with eight or nine bristles (posterior two bristles hirsute, others mostly with short stout spines, but some with proximal hairs and slender distal spines). A single bare bristle on posterior margin interpreted herein to be epipodial bristle. Limb hirsute medially.

Seventh limb (Fig. 6a–c): Each limb with four proximal bristles (two on each side), each with two to four bells, and six terminal bristles (three on each side), each with three to seven bells; all bristles without marginal spines. Terminus with comb of about five teeth opposite two small pegs (one straight, one slightly longer and curved) (Fig. 6c).

Furca: Each lamella with six claws (Fig. 6d, e); 1, 2, and 4 primary claws; claws 3, 5 and 6 secondary claws; claw 4 stouter than claw 3; claw 1 nonarticulated on both lamellae; claw 2 of left lamella articulated (Fig. 6d), of right lamella nonarticulated (probably aberrant because claw 2 of all known species of genus are articulated) (Fig. 6e); remaining claws articulated; claw 1 with teeth forming two rows along proximal two-thirds, some teeth slightly longer than others; claw 2 with few proximal teeth; claw 3 with slender teeth along most of posterior margin; no teeth observed on claw 4; few indistinct teeth on claws 5 and 6; anterior edge and medial surface of right lamella with long hairs; anterior edge of left lamella with few proximal spines; claw 1 or right lamella slightly anterior to claw 1 or left lamella (Fig. 6d).

Bellonci organ (Fig. 6f, g): Elongate, bare, with five proximal segments, broadening distally and with unevenly rounded tip.

Eyes: Lateral eyes with five amber-colored ommatidia (Fig. 6f). Medial eye larger than lateral eye, bare, with scattered brown pigment (Fig. 6f, g).

Upper lip (Fig. 6i): Rounded with minute spines.

Genitalia (Fig. 6h, j): Oval sclerotized ring on each side of body anterior to furca.

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limb; e, Medial view of right sixth limb; f, Lateral view of left sixth limb without endites I and II; g, Medial view of endites II and III of left sixth limb. Abbreviations: Arabic numbers, numbers assigned to joints; Roman numerals, numbers assigned to endites. Scale bar represents 0.05 mm for c, and 0.02 mm for a, b, d–g.

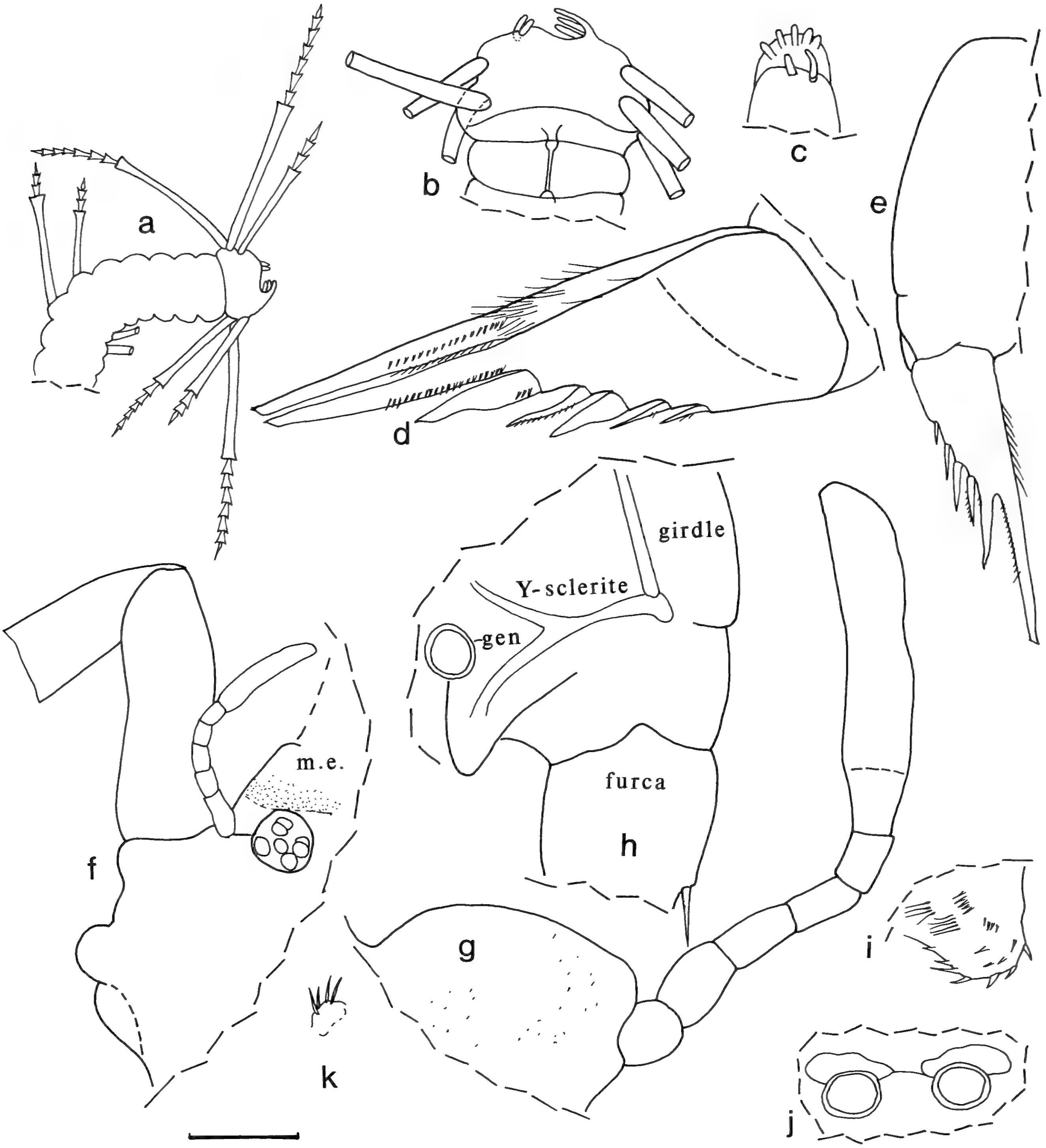

Fig. 6. *Dantya ferox,* holotype, adult female, USNM 193645: a, Seventh limb; b, Detail from a; c, Tip of seventh limb viewed from peg side (this limb not limb shown in a); d, Medial view of claw 1 of right lamella of furca and lateral view of left lamella; e, Posterior of body with right lamella of furca; f, Anterior of body showing medial eye, Bellonci organ, left lateral eye, and joints 1 and 2 of right first antenna; g, Medial eye and Bellonci organ; h, Posterior of body showing girdle, Y-sclerite, left genital organ, and proximal part of left lamella of furca; i, Upper lip, anterior to right; j, Ventral view of both genitalia; k, Brush organ of right side. Abbreviations: gen, genital organ; m.e., medial eye. Scale bar represents 0.1 mm for e, 0.05 mm for a, c, d, f, h–k, and 0.02 mm for b, g.

Brush-like organ (Fig. 6k): Four or five minute bristles anterior to Y-sclerite.

Posterior of body (Fig. 6e): Evenly rounded, bare.

Y-sclerite (Fig. 6h): Branching distally.

Comparisons.—*D. ferox* differs from previously described species of *Dantya* in lacking a dorsal bristle on the second joint of the first antenna. In lateral view the carapace of *D. ferox* resembles that of *D. magnifica,* but lacks the knob-like processes present on the surface of that species. Also, the exopodite of the mandible of *D. ferox* is about one-third the length of the dorsal margin of the first endopodial joint, and is minute on *D. magnifica.*

Acknowledgments

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LAMELLIFORM STRUCTURES ON THE PROBOSCIS OF *PENICULUS* AND *METAPENICULUS* (COPEPODA: PENNELLIDAE)

Raul Castro Romero and Hernan Baeza K.

Abstract.—Two pairs of laminae, at the proboscis base ventral surface were discovered in adult and chalimus IV female stage of *Peniculus* specimens. One pair of these structures is present at the proboscis base of the premetamorphosing female of *Metapeniculus*.

The laminae of *Peniculus* are narrow, those of *Metapeniculus* wide. These laminae are described and illustrated; their importance for the copepod and its taxonomy are discussed.

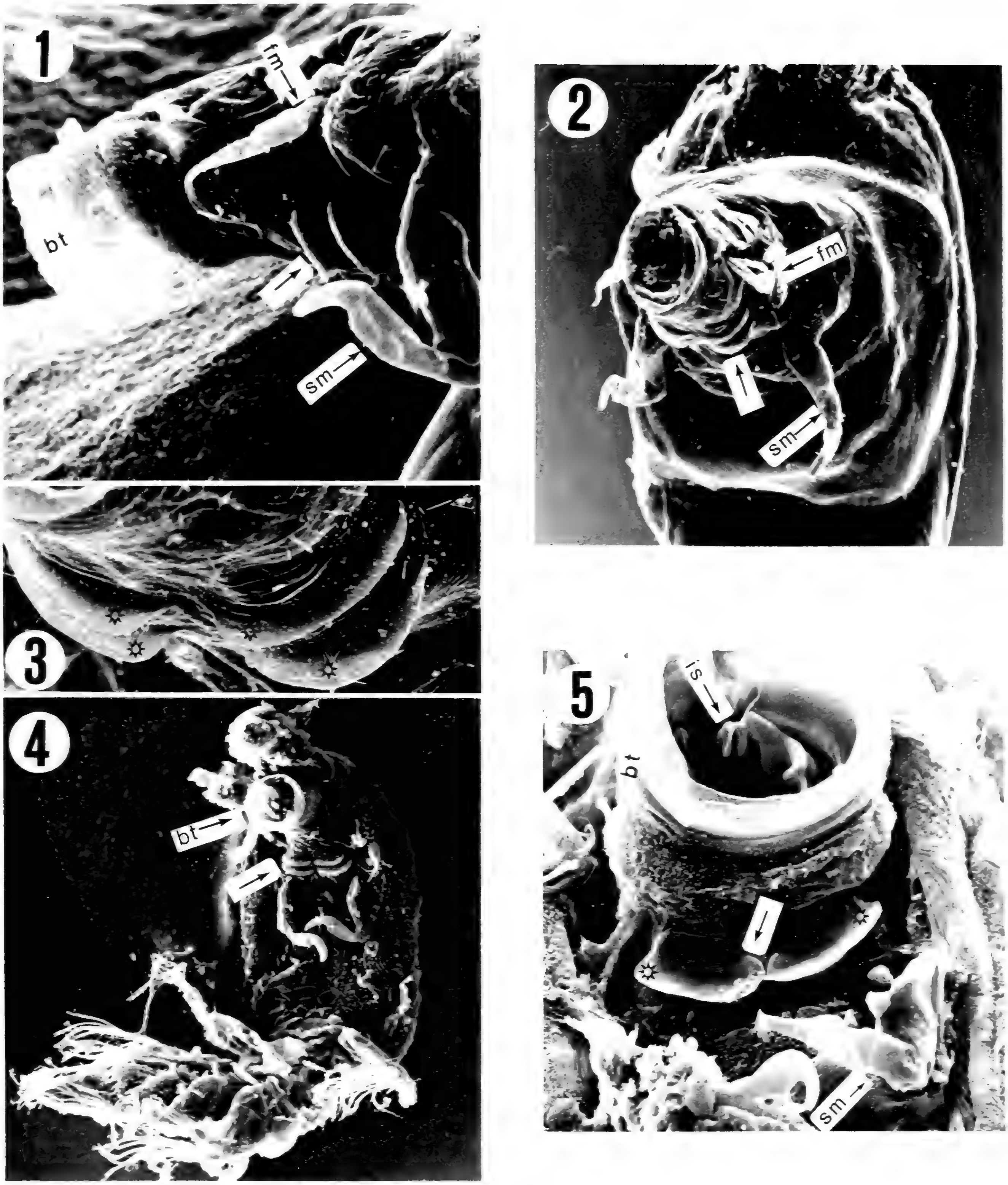
The taxonomy of the Pennellidae Burmeister, 1835 (Copepoda: Siphonostomatoida), which includes parasites on teleosts and some on Balaenoptera (e.g., *Pennella* Oken, 1816) has some problems at both the generic and specific levels. The problems are due to the lack of good discriminant characters, and to the fact that we do not possess accurate and detailed description of the appendages for the majority of pennellid species. The characters used at present (e.g., buccal appendages, leg armament) are more or less uniform throughout the family, and have little, if any discriminant value. The morphology of the anterior part of the body, one of the most commonly used taxonomic characters, shows great intraspecific variability according to the specific attachment site, as has been shown by Hogans (1986) for *Pennella instructa* Wilson, 1917 and by Bellwood (1981) for *Cardiodectes spiralis* Bellwood, 1981.

The taxonomy of *Peniculus* von Nordmann, 1832 is not clear, and is made more difficult by the lack of external characters that facilitate differentiation of the species and that indicate their relationships with other genera of the family, especially with *Metapeniculus* Castro & Baeza, 1985, which is very close morphologically. Kabata & Wilkes (1977) suggest that *P. fissipes* Wilson, 1917 is probably a synonym of *P. fistula* von Nordmann, 1832, this being only one example of the taxonomic problems within this genus.

We searched for new features that could be useful in clarifying the interspecific and intergeneric differences among the pennellids, as well as in establishing intergeneric relationships. We studied some specimens of *Peniculus* von Nordmann, 1832 and *Metapeniculus antofagastensis* Castro & Baeza, 1985, and discovered lamelliform structures on the ventral surface of the buccal cone of *Peniculus* and *M. antofagastensis,* which are illustrated, described, and their importance for the copepods and their taxonomy discussed.

Methods.—*Peniculus* specimens were taken from different host species; adult females from *Hemilutjanus macrophthalmus* (Tschudi, 1845), *Mugiloides chilensis* (Mol.), and *Sciaena fasciata* (De Buen); chalimus IV from *Eleginops maclovinus* (Val.). The premetamorphosing female of *M. antofagastensis* was collected from the type host *Anisotremus scapularis* (Tschudi).

The material was fixed and preserved in formalin (5%) and/or alcohol (70%). Some specimens, fixed as described above, were dehydrated by critical point drying, coated with gold, and examined under SEM Auto-



Figs. 1–5. *Peniculus* sp.: 1, Adult ♀ buccal area, lateral view, ×400; 2, Adult ♀ cephalothorax, ventrofrontal view, ×200; 3, Adult ♀ detail of laminae, ×800; 4, Chalimus 4 ♀, ventral view, showing position of laminae on proboscis ventral surface, ×98; 5, *Metapeniculus antofagastensis*, premetamorphosing ♀, ventral view, ×400. Abbreviations: bt—buccal tube; fm—first maxilla; is—intrabuccal stylet; sm—second maxilla. Laminae indicated by arrows and asterisks.

scan at 20 Kv acceleration. To prevent possible damage to the copepod surface no special cleaning agents were used.

Results.—*Peniculus* sp. (Figs. 1–4): The female specimens examined, regardless of their stage of development (adult and chalimus IV), and the identity of their hosts, bear on the ventral surface, near the base of the buccal cone, two pairs of smooth, narrow laminae with rounded margins. The two pairs are separated from each other by a short gap, and the two members of each pair are slightly separated from each other.

Metapeniculus antofagastensis (Fig. 5): Free living, not metamorphosed, females examined bear on the ventral surface, near the base of the buccal cone, a single pair of laminae, smooth, wide, and with entire margins. The two members of the pair are separated from each other near the midventral line.

Discussion.—The existence of armament on the ventral surface of the pennellid buccal cone is not widely known. Kabata (1963) reported the presence of "serrated lamellae" on the buccal cone of *Lernaeenicus sprattae,* and later Kabata (1979) modified this description to "denticles". These findings were corroborated by Schram (1979). Similar denticles were found by Kabata (1965), in *Lernaeocera centropristi.* In the same paper, Kabata mentioned the presence of transverse "wrinkles" on the buccal cone of *Lernaeocera branchialis* (possibly long laminae). Thomsen (1949) found small "denticles" ("finisimos dientecitos") in *Trifur tortuosus,* and Castro & Baeza (1985) confirmed his finding of "small squamiform sclerites". We add to those records two pairs of long laminae in *Peniculus* and one such pair in *Metapeniculus.*

In view of these findings it is reasonable to assume that structures of this kind may be present in other genera of Pennellidae. The differences among them, in number, shape etc. might be adaptations to their respective microhabitats and to the function they have evolved to fulfil. The two pairs of laminae in *Peniculus* might assist in food intake by collecting solid particles and liquid and facilitating their ingestion. They might also be of some assistance in the process of penetration of the host tissues by the buccal complex.

The same is true of *Metapeniculus,* a genus with microhabitat similar to that of *Peniculus.*

The reduction in number of laminae, and the increase in their size, could be indicative of a functional improvement of those structures in *Metapeniculus,* according to their similar microhabitat shared with *Peniculus.*

The lamelliform structures show a clear difference between *Metapeniculus* (with one pair of laminae) and *Peniculus* (with two pairs of laminae). This adds to the differences between these genera in their thoracopod number (four pairs in *Peniculus* and three in *Metapeniculus*).

Without any doubt the discovery of lamellae in these two genera will be of great help in separating specimens of *Peniculus* and *Metapeniculus* which are very close in external gross morphology, and will help in determining generic relationships within the family. The presence or absence of this structure and their possible variability must be studied for all the species assigned to *Peniculus,* which can give us a clue for species differentiation, and the validity of some *Peniculus* species whose taxonomic status is not clear.

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ACONTIOPHORUS EXCAVATUS, A NEW SPECIES (COPEPODA: SIPHONOSTOMATOIDA) ASSOCIATED WITH THE SOFT CORAL *DENDRONEPHTHYA* (ALCYONACEA) IN THE INDO-PACIFIC

Arthur G. Humes

Abstract.—A new species of siphonostomatoid asterocherid copepod, *Acontiophorus excavatus*, is described from Madagascar, the Philippines, and the Moluccas, where it is associated with the alcyonaceans *Dendronephthya mucronata* and *D. koellikeri*. The new copepod, though closely related to *Acontiophorus bracatus* from the Mediterranean, may be distinguished by the excavated outer margin of the first exopod segment of leg 1 and by the presence of only two small dentiform projections between the terminal setae on the free segment of leg 5.

Many poecilostomatoid and siphonostomatoid copepods are associated with shallow-water cnidarians in the Indo-Pacific. While the poecilostomatoid associates of Alcyonacea have received considerable attention in recent years (e.g., Humes 1975, 1980, 1982; Humes & Dojiri 1979a, 1979b, 1979c; Humes & Stock 1973), the siphonostomatoid copepods associated with these hosts are poorly known. The purpose of this work is to describe a new widely distributed asterocherid copepod living as an associate of soft corals belonging to the genus *Dendronephthya* in the Indo-Pacific.

Materials and Methods

The host alcyonaceans were isolated in plastic bags immediately after collection. Later they were soaked for 1–2 hours in sea water with 5% ethanol, rinsed thoroughly, and the sea water passed through a fine net (about 120 holes per 2.5 cm). The copepods were then recovered from the sediment retained in the net.

The copepods were studied using the wooden slide/lactic acid technique described by Humes & Gooding (1974). Measurements were made on specimens in lactic acid. All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The abbreviations used are: A_1 = first antenna, A_2 = second antenna, and P_1 = leg 1.

Order Siphonostomatoida Thorell, 1859
Family Asterocheridae Giesbrecht, 1899
Genus *Acontiophorus* Brady, 1880
Acontiophorus excavatus, new species
Figs. 1–23

Type material.—43 ♀♀, 70 ♂♂ from *Dendronephthya mucronata* (Pütter), in 25 m, N of Ankazoberavina, near Nosy Bé, NW Madagascar, 13°27.6′S, 47°58.2′E, 24 Aug 1967. Holotype female, allotype, and 103 paratypes (38 ♀♀, 65 ♂♂) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Other specimens.—18 ♀♀, 43 ♂♂ from *Dendronephthya koellikeri* Kükenthal, in 25 m, southern shore of Goenoeng Api, Banda Islands, Moluccas, 04°32′05″S, 129°52′30″E, 26 Apr 1975; 3 ♀♀, 2 ♂♂ from same host, locality, and date; 5 ♀♀, 9 ♂♂, and 9 copepodids from *Dendronephthya koellikeri*, in 10 m, Poelau Gomumu, S of Obi, Moluccas, 01°50′00″S, 127°30′45″E, 30 May 1975; 5 ♀♀ from *Dendronephthya* sp., in 17 m, southwestern shore of Goenoeng Api, Banda Islands, 04°31′45″S, 129°51′55″E, 30 Apr 1975; 1 ♀ from unidentified alcyonacean, probably *Dendronephthya,* in 30 m, Bohol Island, Philippines, 10°17.9′N, 124°10.9′E, 21 Aug 1975.

Female.—Body (Fig. 1) with broad prosome. Length 1.10 mm (0.99–1.19 mm) and greatest width 0.56 mm (0.51–0.59 mm), based on 10 specimens. Greatest dorsoventral thickness 0.35 mm. Epimeral areas of segments bearing legs 1–3 pointed, those of segment bearing leg 3 especially so. Segment bearing leg 4 much smaller than preceding segment and rounded laterally, with only slight point. Ratio of length to width of prosome 1.22:1. Ratio of length of prosome to that of urosome 2.0:1.

Segment bearing leg 5 (Fig. 2) 78 × 101 μm, with small scalelike spines along both lateral margins. Genital segment 172 μm long, 200 μm wide at small anterior rounded expansions, and 185 μm wide posteriorly. Genital areas situated dorsolaterally in front of middle of segment. Each area (Fig. 3) with two small setae, 12 μm and 4 μm. Two postgenital segments from anterior to posterior 49 × 123 μm and 161 × 126 μm. Elongate anal segment, more than twice as long as preceding segment, with small scalelike spines along both lateral margins. Posteroventral border of anal segment smooth.

Caudal ramus (Fig. 4) 47 × 57 μm, wider than long, ratio 1:1.22. Outer lateral seta, lightly feathered, placed dorsally and subterminally, 209 μm. Dorsal seta 55 μm, smooth, with proximal third broader than distal two-thirds. Outermost terminal seta 265 μm, innermost terminal seta 308 μm, and two median terminal setae 297 μm (outer) and 374 μm (inner), all feathered. Inner median terminal seta swollen. Ramus with outer margin having several small scalelike spines and few distal setules, inner margin with several distal setules.

Dorsal surface of body without visible sensilla.

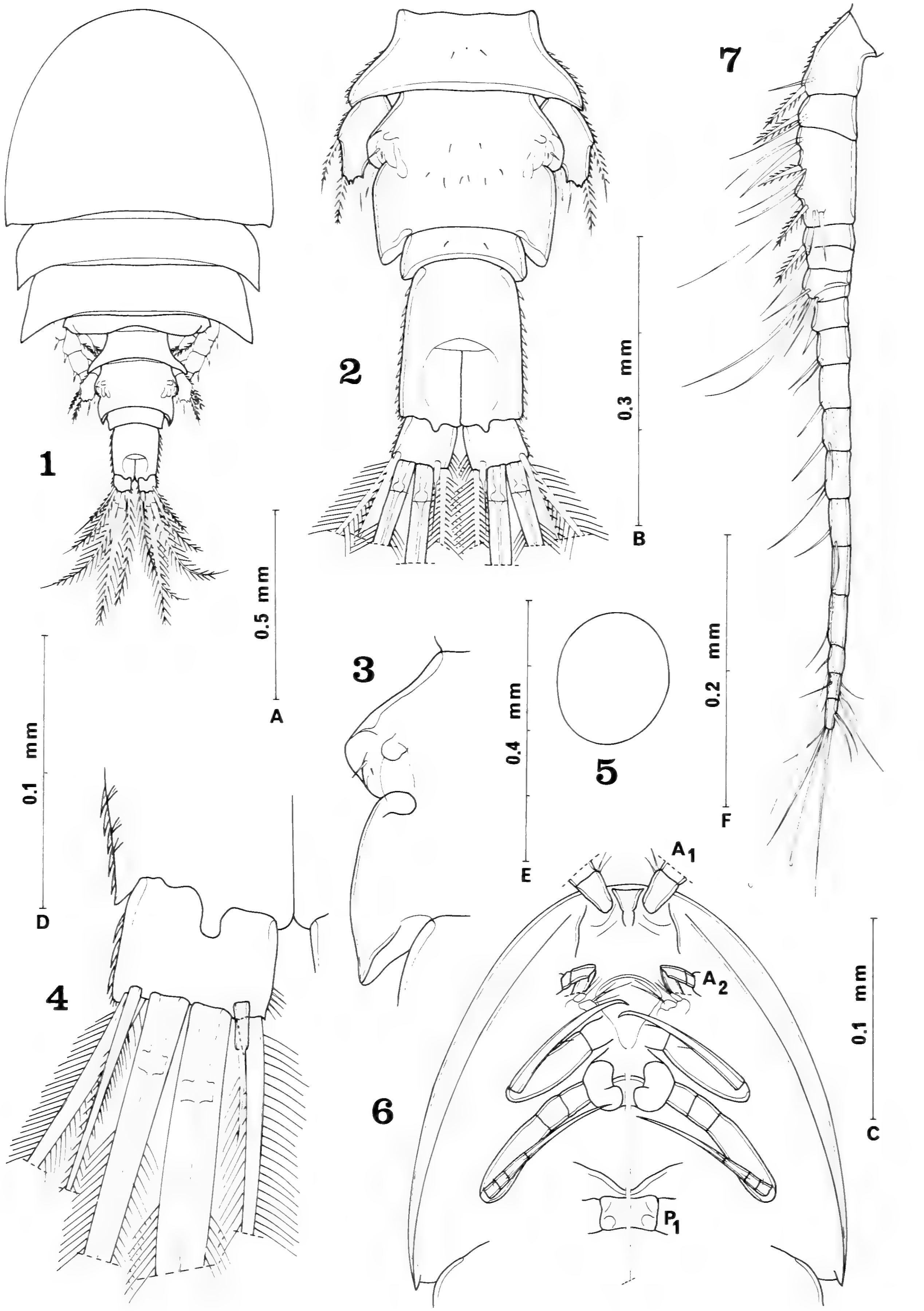
Egg sac empty or incomplete in most specimens. Two egg sacs with single egg 195 × 164 μm (Fig. 5).

Rostrum (Fig. 6) weakly developed. First antenna (Fig. 7) slender, 475 μm long, 17-segmented. Lengths of its segments (measured along their posterior nonsetiferous margins): 26 (68 μm along anterior margin), 25, 60, 26, 11, 8, 19, 29, 29, 29, 30, 30, 34, 36, 15, 15, and 20 μm, respectively. Formula: 2, 2, 10, 2, 5, 1, 1, 2, 2, 2, 2, 2, 1, 2 + 1 aesthete, 2, 3, and 5 + 1 aesthete. Aesthete on segment 14 172 μm long. Certain setae on segments 1–4 subspiniform and having lateral setules. First segment with small spinules along anterior edge.

Second antenna (Fig. 8) with short coxa and elongate basis (greatest length 99 μm) with small spinules on inner margin. Exopod 1-segmented, slender, length 47 μm, with small inner smooth seta and long terminal barbed seta 71 μm long, and having setules along outer side as shown. Endopod 2-segmented, first segment 60 μm long and unarmed, second segment 40 μm long, bearing one seta proximally, one seta near midregion, and two terminal setae very unequal in length, longer of these 138 μm. Fine ornamentation as in Fig. 8.

Siphon (Fig. 9) long and slender, 590 μm long, reaching nearly to posterior rim of intercoxal plate of leg 3.

Mandible (Fig. 10) with 1-segmented palp bearing one small smooth subterminal seta and very long feathered terminal seta. Masticatory part of mandible smooth, elongate, styliform. First maxilla (Fig. 11) with two lobes, outer smaller lobe with three setae, larger inner lobe with five setae, two plumose, two elongate smooth, and one smaller smooth seta. Few setules on inner angle of outer lobe. Second maxilla (Fig. 12) with unarmed basal segment, bearing recurved claw armed with two setae near its midregion and having recurved tip (Fig. 13). Max-



Figs. 1–7. *Acontiophorus excavatus,* new species, female: 1, dorsal (scale A); 2, urosome, dorsal (B); 3, genital area, dorsal (C); 4, caudal ramus, dorsal (D); 5, egg, ventral (E); 6, cephalosome, ventral (E); 7, first antenna, dorsal (F).

illiped (Fig. 14) with two short proximal segments, distal of these with one minute inner seta. Third segment elongate and unarmed. Segments 4, 5, and 6 forming part of "claw", fourth segment having one seta, fifth segment two setae, and sixth segment one seta. Claw elongate, 112 μm, recurved, its proximal third swollen.

Ventral region between maxillipeds and first pair of legs not protuberant and having widely diverging U-shaped sclerotization in front of intercoxal plate of leg 1 (Fig. 6).

Legs 1–4 (Figs. 15–18) biramous, with 3-segmented rami throughout. Formula for armature as follows (Roman numerals indicating spines, Arabic numerals representing setae):

P_1 coxa 0-1 basis 1-I exp I-1; I-1; III,2,3
enp 0-1; 0-2; 1,2,3
P_2 coxa 0-1 basis 1-0 exp I-1; I-1; III,I,4
enp 0-1; 0-2; 1, 1 + I,3
P_3 coxa 0-1 basis 1-0 exp I-1; I-1; III,I,3
enp 0-1; 0-2; 1,I,3
P_4 coxa 0-1 basis 1-0 exp I-1; I-1; III,I,3
enp 0-1; 0-2; 1,I,2

Basis of leg 1 with inner barbed spine 36 μm, small spinules adjacent to its insertion. First segment of exopod of leg 1 with outer margin excavated (Fig. 15). Coxa of leg 2 with outer pectinate fringe (Fig. 16). Endopod of leg 4 (Fig. 18) with inner margins of segments having slender spinules rather than hairlike setules as in legs 1–3.

Leg 5 (Fig. 19) with oval free segment 76 × 50 μm, placed ventrally, armed from inner to outer with two smooth spines 30 μm and 25 μm, short smooth seta 26 μm, and two longer weakly feathered setae 60 μm and 52 μm. Adjacent "dorsal" seta, here inserted ventrally, smooth, 40 μm. Pair of small dentiform processes between two terminal setae. Outer margin of segment with small scalelike spines.

Leg 6 represented by two small setae on genital area (Fig. 3).

Color of living specimens in transmitted light pinkish red, eye red.

Male.—Body (Fig. 20) with prosome less broad than in female. Length 0.71 mm (0.69–0.74 mm) and greatest width 0.32 mm (0.30–0.33 mm), based on 10 specimens. Greatest dorsoventral thickness 0.21 mm. Epimera of segment bearing leg 1 rounded, those of segments bearing legs 2 and 3 somewhat pointed but less prominent than in female. Segment bearing leg 4 relatively wider than in female and more pointed. Ratio of length to width of prosome 1.62:1. Ratio of length of prosome to that of urosome 2.14:1.

Segment bearing leg 5 (Fig. 21) 60 × 120 μm. Genital segment 65 × 122 μm, with well-rounded lateral margins. Three postgenital segments from anterior to posterior 39 × 94, 24 × 78, and 75 × 73 μm.

Caudal ramus 30 × 37 μm, resembling that of female.

Body surface as in female.

Rostrum like that of female. First antenna (Fig. 22) geniculate, 400 μm long, 12-segmented. Lengths of its segments (measured along their posterior nonsetiferous margins): 26 (55 μm along anterior margin), 22, 49, 29, 2, 5, 8, 66, 29, 52, 42, and 39 μm, respectively. Formula: 2, 2, 10, 2, 5, 1, 1, 6, 2, 1, 1 + 1 aesthete, and 6. Second antenna, siphon, mandible, first maxilla, second maxilla, maxilliped, and ventral area between maxillipeds and first pair of legs as in female.

Legs 1–4 as in female.

Leg 5 similar to that of female but free segment smaller, 42 × 28 μm.

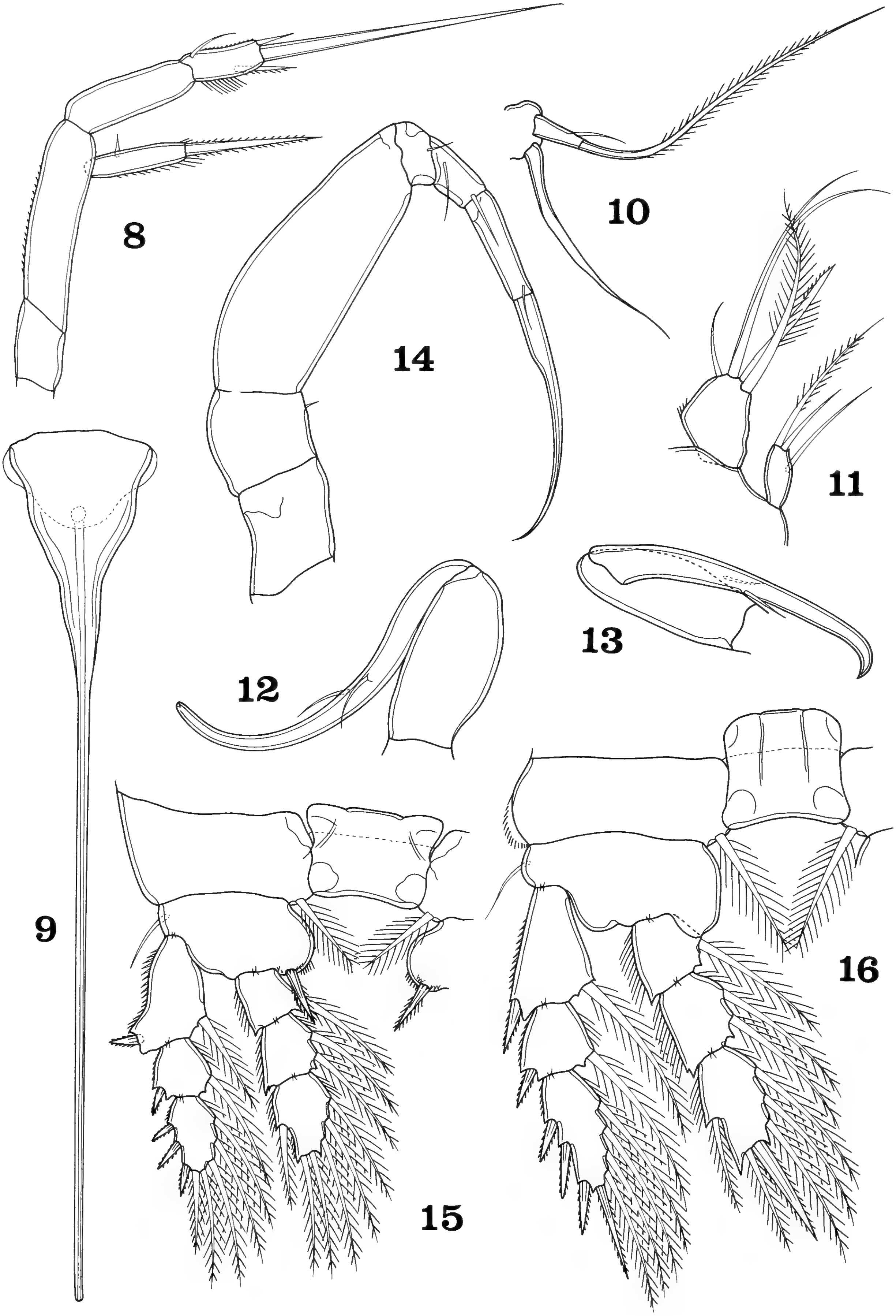
Leg 6 (Fig. 23) represented by 2 unequal setae 10 μm and 31 μm.

Spermatophore unknown.

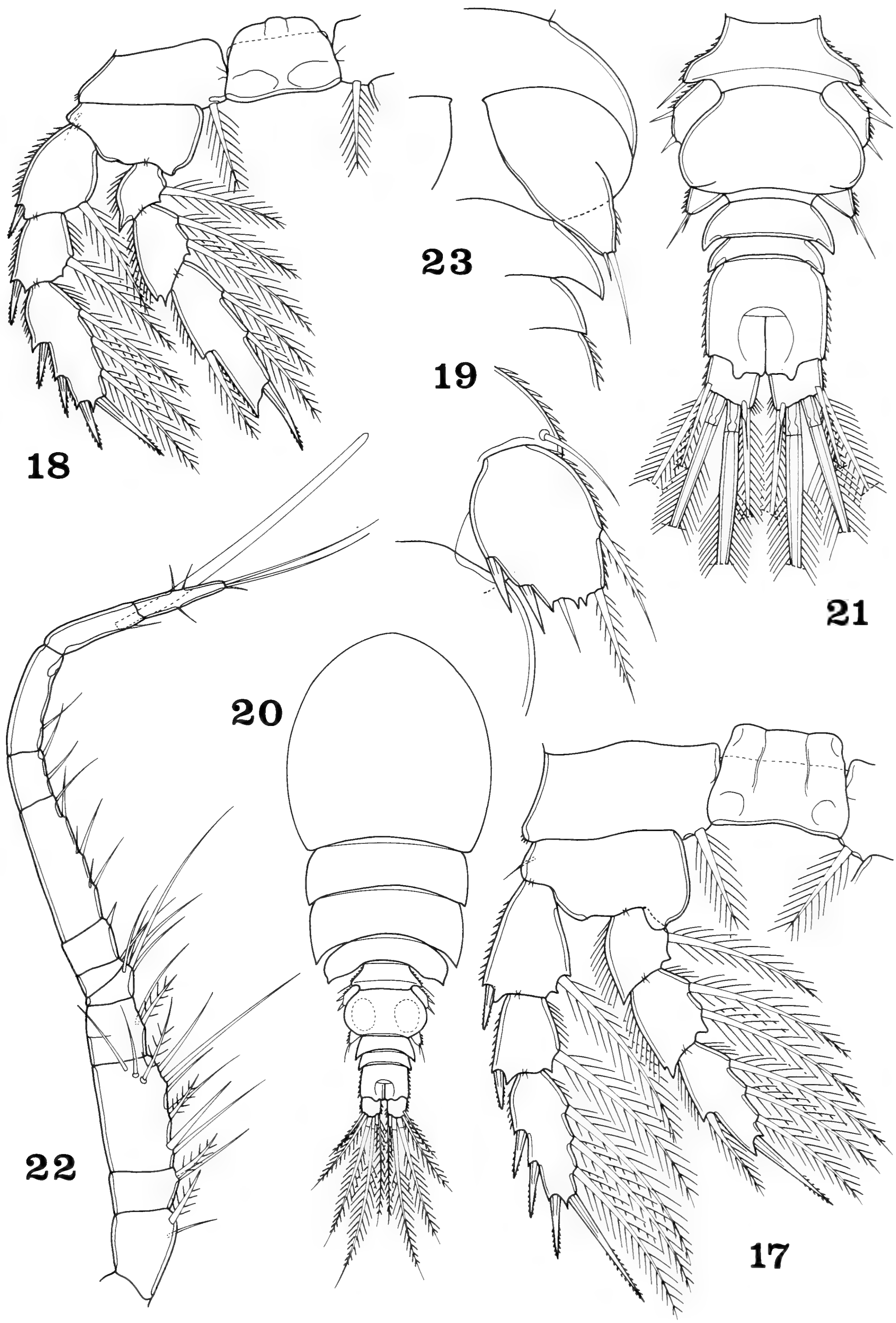
Color of living specimens in transmitted light opaque light tan, eye red.

Etymology.—The specific name *excavatus,* Latin meaning hollowed out, refers to the excavated outer margin of the first segment of the exopod of leg 1.

Remarks.—Eight species are presently recognized in the genus *Acontiophorus* (not including the very insufficiently described *Acontiophorus angulatus* Thompson, 1888).



Figs. 8–16. *Acontiophorus excavatus,* new species, female: 8, second antenna, inner (scale C); 9, siphon, ventral (F); 10, mandible, anteroventral (F); 11, first maxilla, posterodorsal (C); 12, second maxilla, anterodorsal (F); 13, second maxilla, posteroventral (F); 14, maxilliped, posterior (C); 15, leg 1 and intercoxal plate, anterior (F); 16, leg 2 and intercoxal plate, anterior (F).



Figs. 17–23. *Acontiophorus excavatus,* new species. Female: 17, leg 3 and intercoxal plate, anterior (scale F); 18, leg 4 and intercoxal plate, anterior (F); 19, leg 5, ventral (C). Male: 20, body, dorsal (E); 21, urosome, dorsal (F); 22, first antenna, dorsal (C); 23, leg 6, ventral (D).

Acontiophorus excavatus differs from seven congeners (*A. antennatus* Hansen, 1923, *A. brevifurcatus* Stock, 1966, *A. ornatus* (Brady & Robertson, 1876), *A. maldivensis* Sewell, 1949, *A. scutatus* (Brady & Robertson, 1873), *A. tynani* Eiselt, 1965, and *A. zealandicus* Nicholls, 1944) in that the last two postgenital segments in these species are nearly equal in length.

The new species resembles *Acontiophorus bracatus* Stock & Kleeton, 1963, in having the anal segment much longer than the preceding segment, and in the presence of small scalelike spines along the sides of this segment. However, *A. excavatus* differs from *A. bracatus* (and from all congeners as far as can be determined from published descriptions) in having the outer margin of the first segment of the exopod of leg 1 distinctly excavated (see Fig. 15), and in having two small dentiform processes between the two terminal setae on the free segment of leg 5 (instead of four as in *A. bracatus*).

Both *Acontiophorus excavatus* and *A. bracatus* are associated with alcyonaceans, the former with the nephtheids *Dendronephthya mucronata* and *D. koellikeri* in the Indo-Pacific and the latter with the alcyoniid *Parerythropodium coralloides* (and also the gorgonians *Eunicella stricta* and *Leptogorgia sarmentosa*) in the Mediterranean.

Acknowledgments

The collection of the copepods was made possible in 1967 in Madagascar by a grant (GB 5838) from the National Science Foundation and in 1975 in the Moluccas and the Philippines during the *Alpha Helix* East Asian Bioluminescence Expedition, which was supported by the National Science Foundation under grants OFS 74 01830 and OFS 74 02888 to the Scripps Institution of Oceanography and grant MBS 74 23242 to the University of California, Santa Barbara.

I am indebted to Dr. J. Verseveldt, now deceased, for the identification of the alcyonacean hosts.

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AN UNUSUAL SPECIES OF THE *BALANUS AMPHITRITE* DARWIN COMPLEX (CIRRIPEDIA, BALANIDAE) FROM THE ANCESTRAL COLORADO RIVER DELTA IN WESTERN ARIZONA AND SOUTHEASTERN CALIFORNIA

Victor A. Zullo and Anna V. Buising

Abstract.—Shells and opercular plates of *Balanus canabus,* new species, form shell hashes in the upper Cenozoic Bouse Formation of western Arizona and southeastern California. The thin, columnar shells and morphologically variable opercular plates indicate growth of large, crowded colonies in low salinity waters. The vesicular sheath and the overall morphology of the opercular and compartmental plates are characteristic of the genus *Fistulobalanus* Zullo, but the lack of multiple rows of parietal tubes precludes assignment to this genus. *Balanus canabus* is not clearly related to any extant eastern Pacific species, but does resemble the western Pacific species *Fistulobalanus albicostatus* (Pilsbry) and *F. kondakovi* (Tarasov & Zevina) and the Atlantic and Indian Ocean species *F. pallidus* (Darwin).

Barnacle hashes in the Bouse Formation of western Arizona and southeastern California (Fig. 1) are formed by the shells of a single species of balanid barnacle. The hashes consist of partially crushed, extremely thin-walled, columnar to tulipiform shells with intact opercular pyramids, together with disarticulated compartmental and opercular plates (Fig. 4e). The new species is remarkable in the thinness of its plates and, particularly, in the unusual growth modifications of its scuta and terga. The carinal margins of the terga and the upper occludent margins of the scuta are reflexed inward through secondary growth, creating an expanded compartment at the apex of the opercular pyramid.

The tubiferous shell wall with numerous transverse septa, the tubiferous basis, the narrow radii with finely denticulate sutural edges, and the well developed scutal adductor ridge, serve to identify this species with the diverse and widespread *Balanus amphitrite* Darwin complex (see Henry & McLaughlin 1975). Although the overall morphology of the opercular plates and the vesicular sheath of the new species are characteristic of the genus *Fistulobalanus* Zullo, the lack of multiple rows of parietal tubes precludes assignment to this genus.

Stratigraphy and Paleoenvironments of the Bouse Formation

The outcrop belt of the Mio-Pliocene Bouse Formation includes more than 3000 km^2 of discontinuous exposure in western Arizona and southeastern California (Fig. 1). Strata now assigned to the Bouse Formation were recognized early in the twentieth century (e.g., Blanchard 1913), but were not formally named until later regional work by Metzger (1968). The Bouse Formation was recently re-examined by Buising (1988) on whose study the following discussion of stratigraphy and sedimentology is based.

Strata of the Bouse Formation are interpreted as documenting transgression of what is now the lower Colorado River trough by waters of the proto-Gulf of California, a tec-

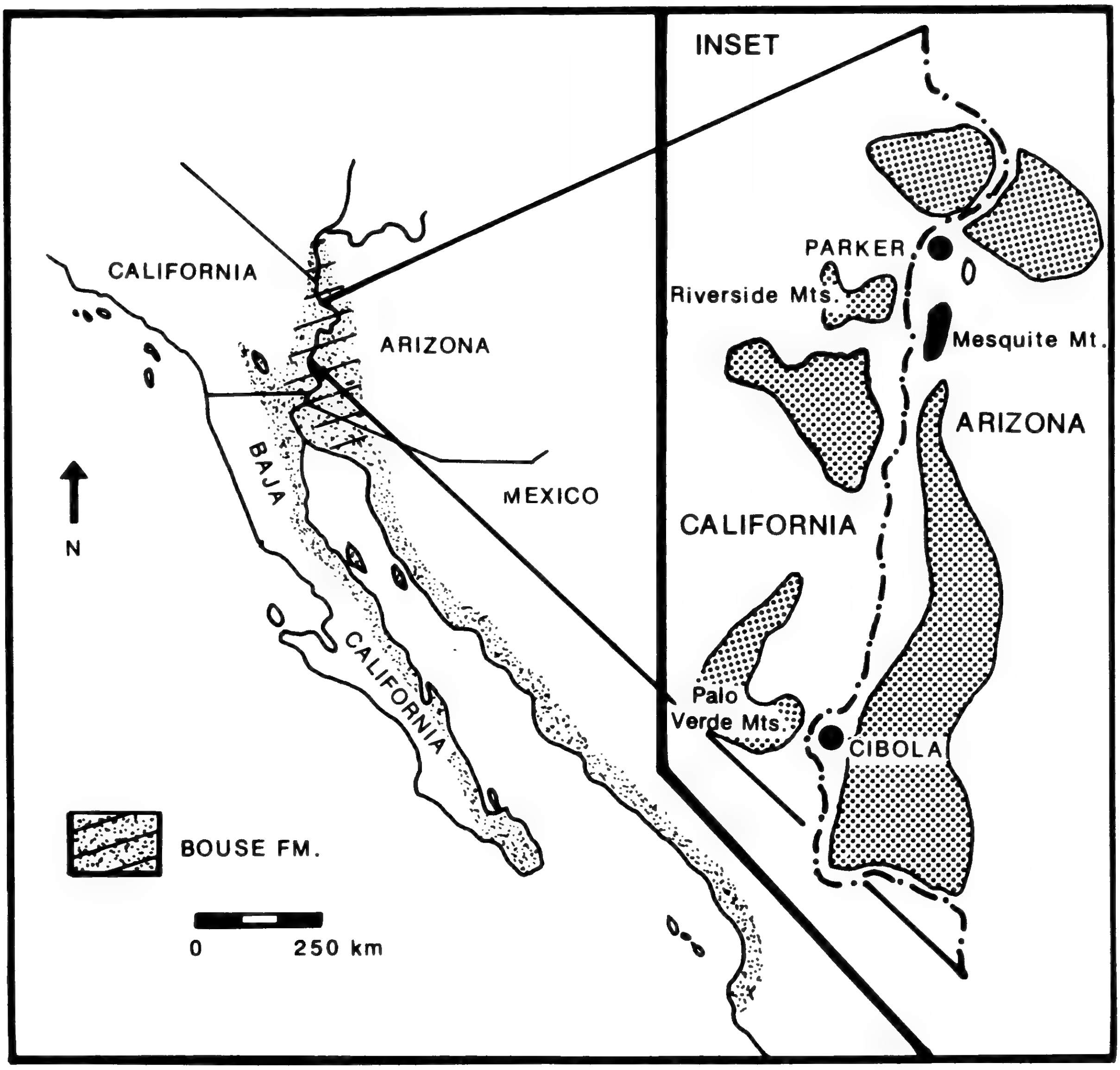

Fig. 1. Distribution of Bouse Formation (cross-hatched) in relation to inferred extent of proto-Gulf outcrop belt (stippled). Inset shows mountain ranges (stippled) of the lower Colorado River region and location of Mesquite Mountain, type locality of *B. canabus* (after Buising 1988).

tonically complex marine embayment that occupied the Gulf of California physiographic province prior to onset of modern spreading- and transform-generated subsidence in that region (Fig. 1). Basal transgressive carbonate of the Bouse Formation overlies pre-Bouse fanglomerate, reflecting inundation of an internally drained alluvial system during proto-Gulf subsidence. The basal carbonate is overlain by fine-grained terrigenous clastic strata recording the southward progradation of the ancestral Colorado River delta into the proto-Gulf. These deltaic facies interfinger laterally with a shoreline complex that includes algal tufa, clastic limestone and barnacle coquina, as well as coarse-grained, terrigenous clastic units derived from the erosion of local island and basin-margin highs. The Bouse Formation is overlain by, and interfingers with trough cross-bedded cobble conglomerates, informally called the Colorado River gravels, that are characterized by a clast assemblage derived from the Colorado Plateau, and are interpreted as recording arrival of the through-going Colorado fluvial channel in approximately its modern position. Although the age of the Bouse Formation remains problematic, recent reevaluation suggests that it was deposited between eight and four million years ago (Buising 1988).

Paleoecology

With the exception of channel lag occurrences, such as those at Mesquite Mountain, and of isolated occurrences in distributary channel siltstone, the barnacles are usually associated with coarse terrigenous clastic units and algal tufa that mark the shoreline of the proto-Gulf (Buising 1988). The proto-Gulf shoreline, which is preserved in essentially its original depositional configuration, was extremely rugged and rocky and, presumably, provided the principal substratum for the barnacles. However, barnacles were not found attached to rocks in the shoreline facies, and the only examples found in life position were attached to algal tufa at a shoreline locality northeast of the type channel lag deposits at Mesquite Mountain (Buising 1988).

The abundance of barnacles, and thinness and morphological variability of their plates, indicate rapid, seasonal growth in waters of lowered salinity. Low salinity waters are also suggested by algal tufa morphology and $^{87/86}$ Sr values of tufa and barnacle shell samples (Buising 1988). The crowded, columnar to tulipiform growth habit suggests that hard substrata suitable for settlement were limited, and that vertical growth was a necessary prerequisite for competition under crowded conditions. In addition, some depositional environments of the Bouse Formation suggest that rapid vertical growth was essential to maintaining the individual above the terrigenous clastic detritus being deposited in the delta system.

It is likely that cyprid larvae were carried into the delta by the advancing salt wedge during the dry season, and settled in dense masses on every available hard substratum. Adult size was probably attained within a single year, as at least two size classes are recognized, appearing to represent separate yearly settlement. The parietes and scuta of the larger size class, which attained an average adult height of one cm, are overgrown by smaller individuals averaging about one-half cm in height. Although the limited use of calcium carbonate in the shell is indicative of growth in lowered salinities, neither size class shows any evidence of the shell corrosion common in such brackish water species as *Balanus eburneus* Gould and *Fistulobalanus pallidus* (Darwin). This is particularly interesting as the larger size class appears to have lived for more than a single year and, thus, long enough for corrosion to occur.

Systematics

Family Balanidae Leach, 1817
(Newman & Ross 1976)
Subfamily Balaninae Leach 1817
(Newman 1980)
Genus *Balanus* Da Costa, 1778
Balanus canabus, new species
Figs. 2–4

Holotype.—Partially crushed opercular pyramid, USNM 423910.

Type locality.—Bouse Formation, west flank of Mesquite Mountain, La Paz County, Arizona.

Diagnosis.—Shell thin, cylindric to tulipiform, with smooth parietes; radii narrow, with steeply sloping summits and denticulate sutural edges; alae extremely broad, with horizontal summits and denticulate sutural edges; sheath vesicular; parietal tubes rectangular, in single row. Scutum very thin, extremely convex or medially sulcate, much taller than broad; external longitudinal striae very fine or absent; articular ridge about one-half length of tergal margin; adductor ridge short, well separated from articular ridge; depressor muscle pit shallow and triangular or absent. Tergum very thin, broad, externally convex, with convex carinal margin and narrow, sometimes deep, spur furrow broadening toward spur; upper carinal margin reflexed inward to form broad in-

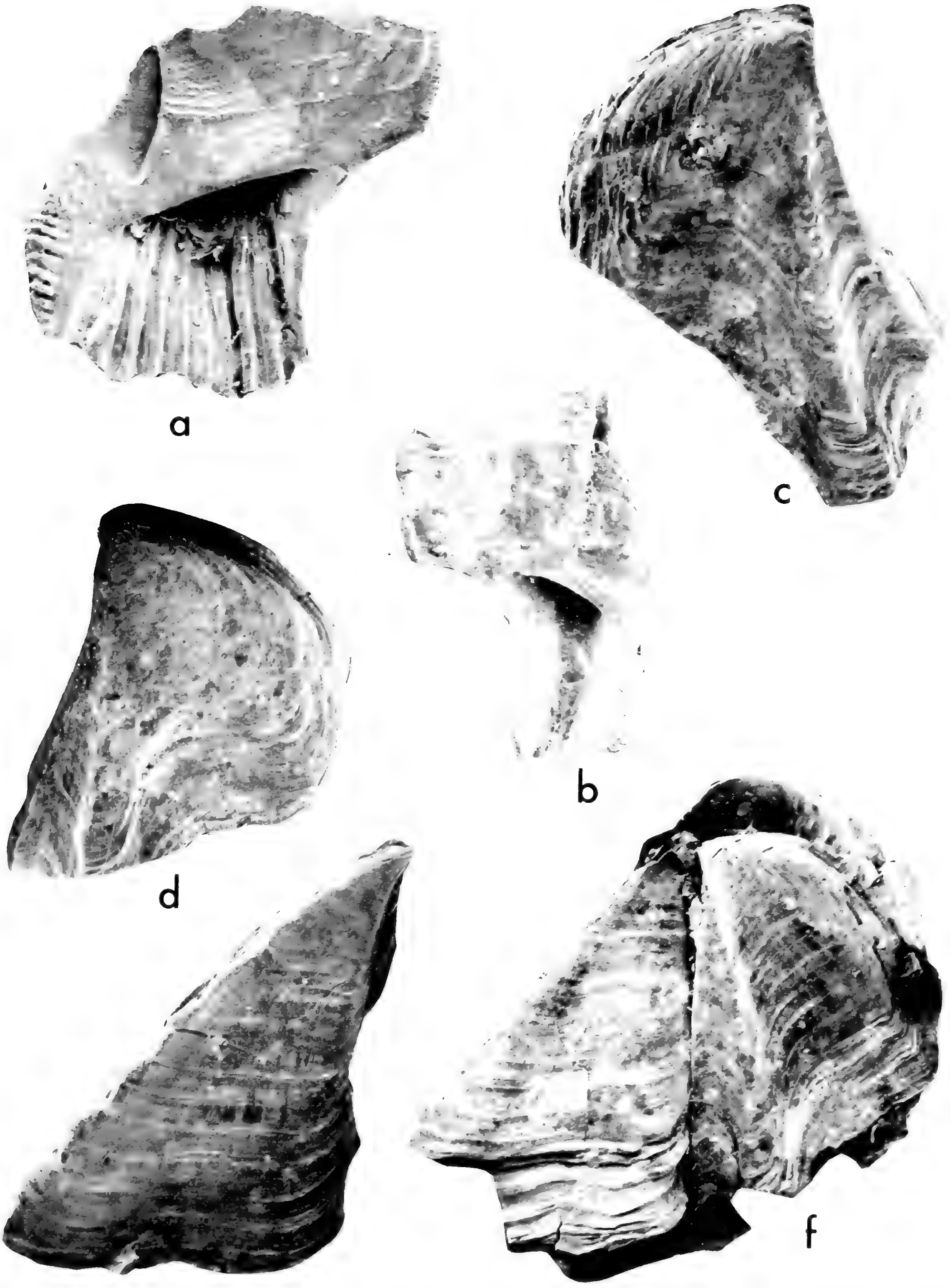

Fig. 2. *Balanus canabus*: a, Interior of lateral plate, paratype USNM 423920, ×27; b, Interior of carinolateral plate, paratype USNM 423921, ×11; c, Exterior of tergum, paratype USNM 423922, ×11; d, Exterior of tergum (lacking spur), paratype USNM 423923, ×12; e, Exterior of scutum, paratype USNM 423924, ×12; f, Articulated opercular pyramid, holotype USNM 423910, ×12.

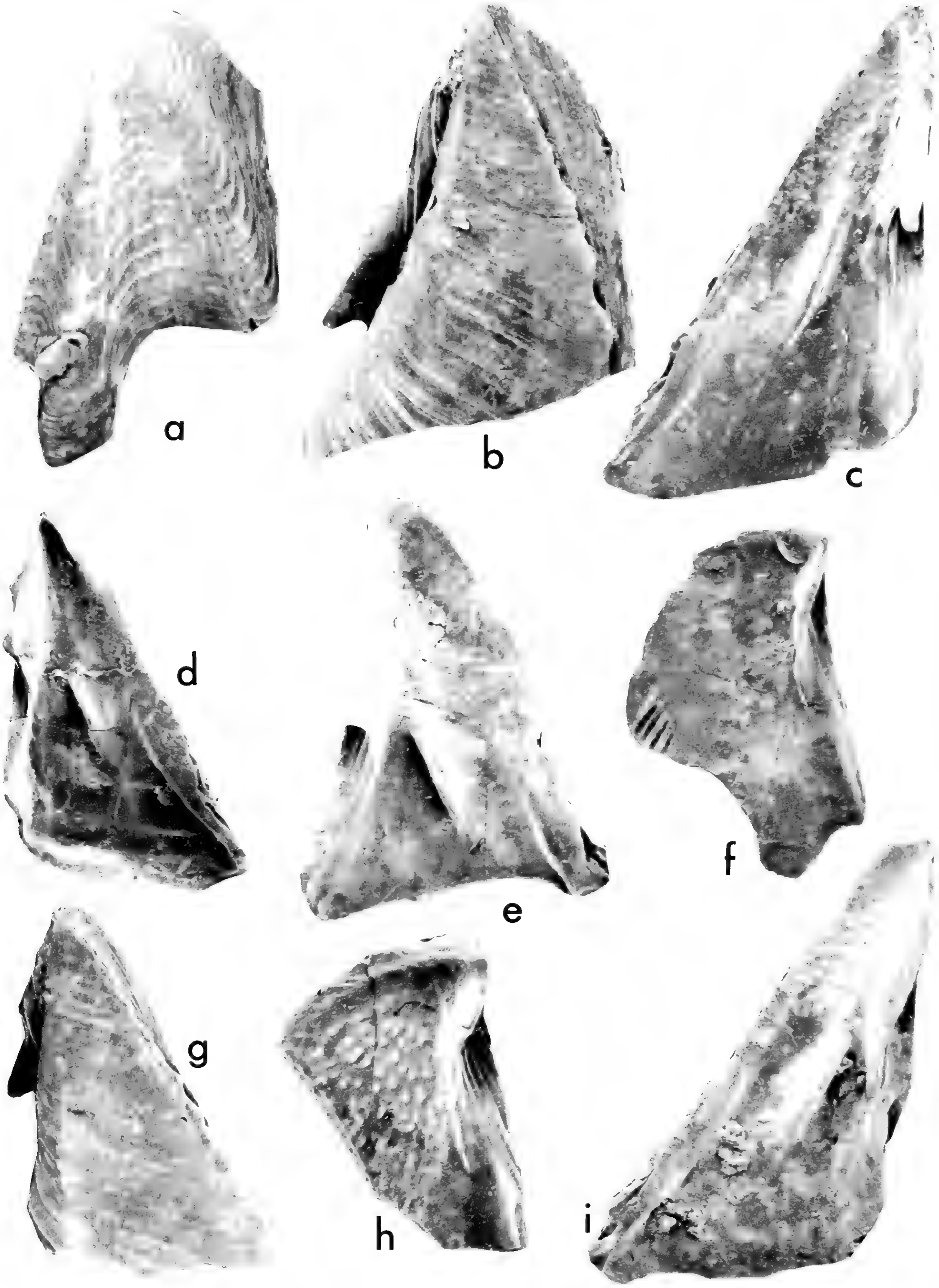

Fig. 3. Opercular plates of *Balanus canabus*: a, Exterior of tergum, paratype USNM 423911, ×12; b, Exterior of apical half of scutum showing secondary extension of occludent margin (on right side), paratype USNM 423912, ×18; c, Interior of scutum, paratype USNM 423913, ×12; d–e, Interiors of scuta, paratypes USNM 423914 through 423915, ×16; f, Interior of tergum, paratype USNM 423916, ×12; g, exterior of scutum, paratype USNM 423917, ×12; h, Interior of tergum (lacking spur) showing apical compartment, paratype USNM 423918, ×12; i, Interior of scutum, paratype USNM 423919, ×14.

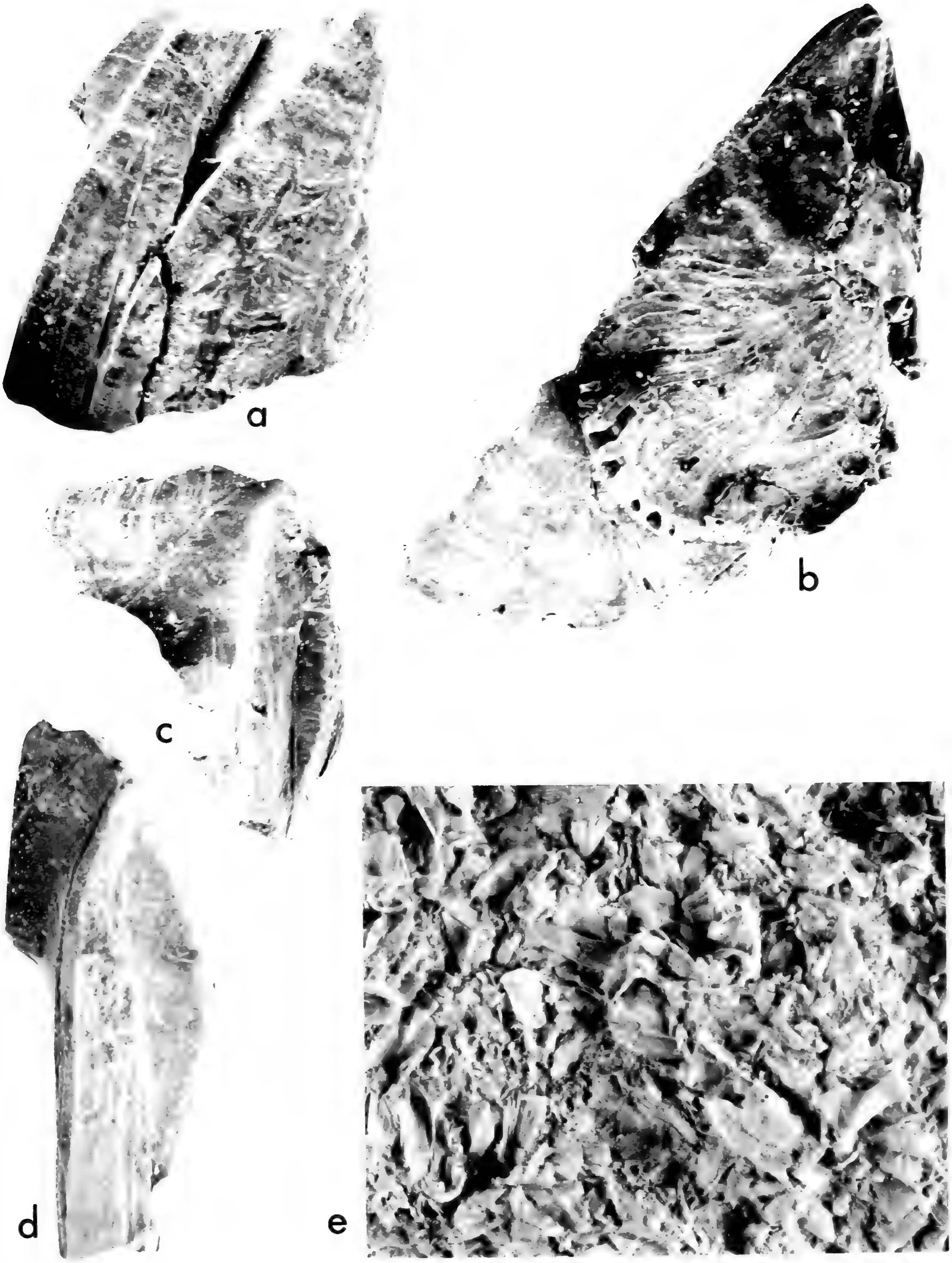

Fig. 4. *Balanus canabus*: a, Articulated lateral and carinolateral plates, paratype USNM 423925, ×25; b, Basis of second generation individual attached to scutum, paratype USNM 423926, ×19; c, Exterior of carinolateral showing distal extension of ala, paratype USNM 423927, ×11; d, Carinolateral of cylindric individual, paratype USNM 423928, ×11; e, Barnacle hash from channel lag deposit of type locality, paratype lot USNM 423929, ×1.5.

ternal shelf; spur slightly longer than wide, basally subtruncate; distance from basiscutal angle to spur less than or equal to spur width; basal margin straight to concave on both sides of spur, not deeply excavated.

Material.—Twenty-seven shells with or without opercular plates; over 1000 disarticulated compartmental plates; 77 whole or partial scuta; 65 whole or partial terga.

Disposition of types.—Holotype USNM 423910, paratypes USNM 423911 through 423928, and paratype lot USNM 423929 are deposited in the collection of the Department of Paleobiology, National Museum of Natural History, Washington, D.C.

Geologic and geographic range.—Late Cenozoic (probably latest Miocene or Pliocene), Bouse Formation, southeastern California and western Arizona.

Etymology.—The specific name is derived from the Greek *kanabos,* meaning "a mere skeleton," and refers to the extremely thin shell of this species.

Description.—Shell thin, cylindric to tulipiform in adults, high conic in juveniles, with slightly toothed orifice and smooth parietes; a few specimens show traces of broad, longitudinal color stripes on parietes; radii narrow, not sunken, transversely striate, with steeply sloping summits (70°) and thin, finely crenate, sutural edges; alae very broad, composed of proximal and distal segments separated by incised diagonal line and change in growth pattern; horizontal to convex summits of alae formed by distal segments; alar sutural edges finely crenate; sheath about one-third length of compartmental plate, vesicular, without vesicles in furrow below dependent lower margin; internal parietal ribs prominent, regularly spaced, flat-topped, extending from base to sheath, finely crenate basally; longitudinal parietal tubes large, rectangular, in single row, crossed by numerous, closely spaced, transverse septa; basis calcareous, thin in center and thickening appreciably toward margin, with fine radial tubes bearing few transverse septa.

Scutum thin, narrow, with basal margin two-thirds to three-fourths length of tergal margin; exterior either flat with median longitudinal sulcus or broadly convex; apex often twisted slightly toward tergum; exterior ornamented by broadly spaced major growth ridges forming denticles on occludent margin and numerous, fine, minor growth ridges between major ridges; exterior growth ridges usually crossed by extremely fine longitudinal striae in central part of plate; tergal margin straight to slightly concave, broadly reflected from 45° to 60° from plane of plate; occludent margin convex, sharply inflected in upper half; inflected area of occludent margin often enlarged by secondary growth in apical region; basal margin straight to slightly sinuous; articular ridge prominent, usually about one-half length of tergal margin, forming a broad, flat shelf in upper half, becoming narrow and sharp in lower half, and ending in sharp, downturned hook, partially reflected over deep, narrow, articular furrow; adductor ridge sharp, erect, highest adjacent to adductor muscle pit, variable in length, but usually short, centrally located, and well removed from articular ridge; adductor muscle pit shallow, small, round to oval; a shallow, triangular pit often present on tergal side of adductor ridge; depressor muscle pit either moderately large, shallow and triangular or absent; interior of apical half of scutum rugose.

Tergum thin, convex, broad, with basal margin one-half to two-thirds length of plate; carinal margin convex, usually protuberant apically, sharply inflected in apical half forming internal apical chamber; scutal margin straight to concave, sharply inflected to form flat shelf; basal margin not deeply embayed, straight to concave on either side of spur; exterior ornamented by closely spaced major, and a few interspersed minor, growth ridges; broad area along carinal margin marked by sharply upturned growth lines; carinal side of exterior bearing fine radial striae partially reflecting position of internal depressor muscle crests; spur furrow narrow in apical half, widening toward spur, often very deep; sides of spur furrow not marked by incised lines and not infolded; spur with nearly parallel sides and subtruncate base, placed between one-half its width and distance equal to its width from basiscutal angle, moderately long, about two-ninths length of plate, and narrow, less than one-third width of basal margin; articular ridge nearly erect, high, thin, concave on scutal side, little more than one-half length of scutal margin, and continuous with inflected part of carinal margin forming apical chamber; articular furrow broad, moderately deep; depressor muscle crests short, well developed, closely spaced, usually five in number; interior or tergum markedly rugose in apical half.

Discussion.—Aside from the marked thinness of the compartmental and opercular plates, the features that set the new species apart from other members of the *Balanus amphitrite* complex are those apparently associated with the broadening of the orifice with continued vertical growth under crowded conditions. Development of the tulipiform shell is accomplished through secondary distal growth of the alae rather than widening of the radii. In fact, the steeply sloping radius is in contact with the paries of the adjacent compartment only in the basal third of the shell wall. The opercular pyramid, which occupies most of the orifice, accommodates the increase in orifice diameter through secondary horizontal growth on either side of the aperture formed by the occludent margin of the scutum and the carinal margin of the tergum. This horizontal growth produces a chamber in the apex of the opercular pyramid which is particularly apparent on the interior of the tergum. A similar chamber is seen in terga of the extant western Pacific species *Fistulobalanus albicostatus* (Pilsbry) and *F. kondakovi* (Tarasov & Zevina). The growth form and resulting morphology of *B. canabus* appear to be related both to competition for living space under crowded conditions in an area of limited substrata, and to maintenance of the individual above the sediment that was being deposited in the delta environment.

Although *B. canabus* shares many morphological features with fossil and extant species of *Fistulobalanus,* it lacks multiple rows of parietal tubes in the shell wall and, therefore, cannot be included in the genus. The similarity of the new species to *Fistulobalanus* is striking, however. All of the extant species of the genus are found in brackish waters (Henry & McLaughlin 1975; the habitats of *F. abeli* (Lamy & André) and of *F. patelliformis* (Bruguière) are unknown). Some specimens of *F. pallidus* and *F. kondakovi* lack subsidiary parietal tube rows, and these species often occur in crowded, thin-walled, cylindric masses in brackish water environments (Stubbings 1963; Henry & McLaughlin 1975). The morphology of the opercular and compartmental plates of *B. canabus* is typical of *Fistulobalanus,* especially of *F. pallidus, F. albicostatus* and *F. kondakovi,* and bears less resemblance to species of *Balanus.* The absence of subsidiary parietal tubes may be related to the crowded, columnar growth habit and the conservative use of calcium carbonate in shell construction.

It is possible that *B. canabus* was derived from a *Fistulobalanus* ancestor. The genus extends back to the middle Miocene in the North Atlantic basin (Zullo 1984), and is known from the Pleistocene of Japan (Yamaguchi 1980). However, the two extant species of *Fistulobalanus* known from the eastern Pacific, *F. dentivarians* (Henry) and *F. suturalis* (Henry), bear less resemblance to *Balanus canabus* than do the previously mentioned western Pacific and Atlantic Ocean species.

Among the species of the *B. amphitrite* complex with a single row of parietal tubes, only the extant western Atlantic species *B. eburneus* and *B. subalbidus* Henry possess a vesicular sheath. Like the species of *Fistulobalanus,* both are inhabitants of brackish waters. *Balanus eburneus* differs in having radii with broader, gently sloping summits; prominent, deeply incised external radial striae on the scutum; a scutal adductor ridge that is almost confluent with the articular ridge; and a tergum with a spur fasciole and a markedly concave and usually deeply embayed basal margin on the carinal side of the spur. *Balanus subalbidus* differs in having a broader scutum with the adductor and articular ridges nearly confluent, and a tergum with a spur fasciole and a broader spur.

Locality Descriptions

The type lot of *B. canabus* was obtained from the fine-grained, terrigenous-clastic, deltaic facies of the Bouse Formation on the west flank of Mesquite Mountain, La Paz County, Arizona. At this locality, transported barnacles and barnacle plates occur as a lag deposit in a northerly-trending channel approximately 5 m wide and slightly less than 1 m deep. The channel, filled with green mud, is located at the western terminus of a pink siltstone bed with pervasive, westward-migrating, meter-high, trough cross-beds. The entire complex is interpreted as representing progressive westward migration of a tidally-influenced distributary channel, followed by channel abandonment and infilling by green hypoxic mud (Buising 1988).

Other specimens of *B. canabus* examined for this study were collected in 1961 by Blakemore E. Thomas, San Diego State University, from Bouse Formation outcrops on the north end of the Riverside Mountains, Riverside County, and the Palo Verde Mountains, Imperial County, California.

Acknowledgments

We thank the people and council of the Colorado River Indian Tribes for allowing access to tribal lands in the Mesquite Mountain area for mapping and sampling purposes. Special thanks are extended to Charles Lamb, Weldon Johnson, Curtis Martin and the Colorado River Indian Tribes Museum.

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FIRST INGOLFIELLIDS FROM THE SOUTHWEST PACIFIC (CRUSTACEA: AMPHIPODA) WITH A DISCUSSION OF THEIR SYSTEMATICS

James K. Lowry and Gary C. B. Poore

Abstract.—Two new species of ingolfiellid amphipods, *Ingolfiella australiana* and *I. bassiana* are described from the continental shelf of Bass Strait, southeastern Australia. *Ingolfiella australiana* is similar to some species of the subgenus *Trianguliella* Stock, 1976. *Ingolfiella bassiana* cannot be placed easily into any known subgenus, but shows some similarities to species described from the West Indies and the Canary Islands in the subgenus *Gevgeliella* Karaman, 1959. A re-analysis of sexually dimorphic characters casts doubt on current generic and subgeneric concepts. It is concluded that the ingolfiellidean "eye-lobe" is not homologous with the dorsal pedunculate eyestalk of other peracaridans because of its lateral position. This and other evidence from the Metaingolfiellidae place the ingolfiellidean families within the Gammaridea. The ingolfiellidean maxilliped, carpochelate gnathopod 2, and the entire telson suggest similarities to the leucothooid gammarideans. Retention of shared plesiomorphic characters such as a maxilliped without an ischial endite and an entire telson indicates an early derivation from the amphipodan stem.

The ingolfiellidean amphipods comprise about 30 species in 2 families, Ingolfiellidae and Metaingolfiellidae. Ruffo (1970), Stock (1976, 1977, 1979), Ronde-Broekhuizen & Stock (1987), and Dojiri & Sieg (1987) have reviewed the systematics and zoogeography of the group. Although widely distributed from the deep sea to fresh water and hypogean habitats, ingolfiellideans have not previously been recorded from the Southwest Pacific.

Two new species of small ingolfiellids, described herein, were discovered in 2 of over 200 lots of amphipods sorted from benthic samples taken from the continental shelf and slope of Bass Strait, southeastern Australia. Material is lodged in the Museum of Victoria, Melbourne (NMV) and the Australian Museum, Sydney (AM).

The Ingolfiellidae is a conservative family of three genera (Stock 1976, Ruffo 1985). Few specific differences occur in overall body shape, antennae, mouthparts or peraeopods. Nevertheless, Stock (1976) erected five subgenera within *Ingolfiella*, the largest genus. These are separated largely on the basis of sexually dimorphic differences in the second gnathopod and pleopods. We discuss some of the taxonomic problems associated with these subgenera. We also discuss the phylogenetic placement of the ingolfiellidean group.

Family Ingolfiellidae Hansen, 1903

Ingolfiella australiana, new species
Figs. 1–4

Type specimens.—Holotype, male, 2.3 mm, NMV J12851 with 2 slides, paratype, "female," 2.2 mm NMV J12850 with 2 slides, 34 km SW of King Island, 40°26.7′S 143°41.4′E, Bass Strait, Australia, 85 m, sandy shell, Smith-McIntyre grab, R. Wilson et al. on RV *Tangaroa,* 22 Nov 1981 (NMV station BSS 198).

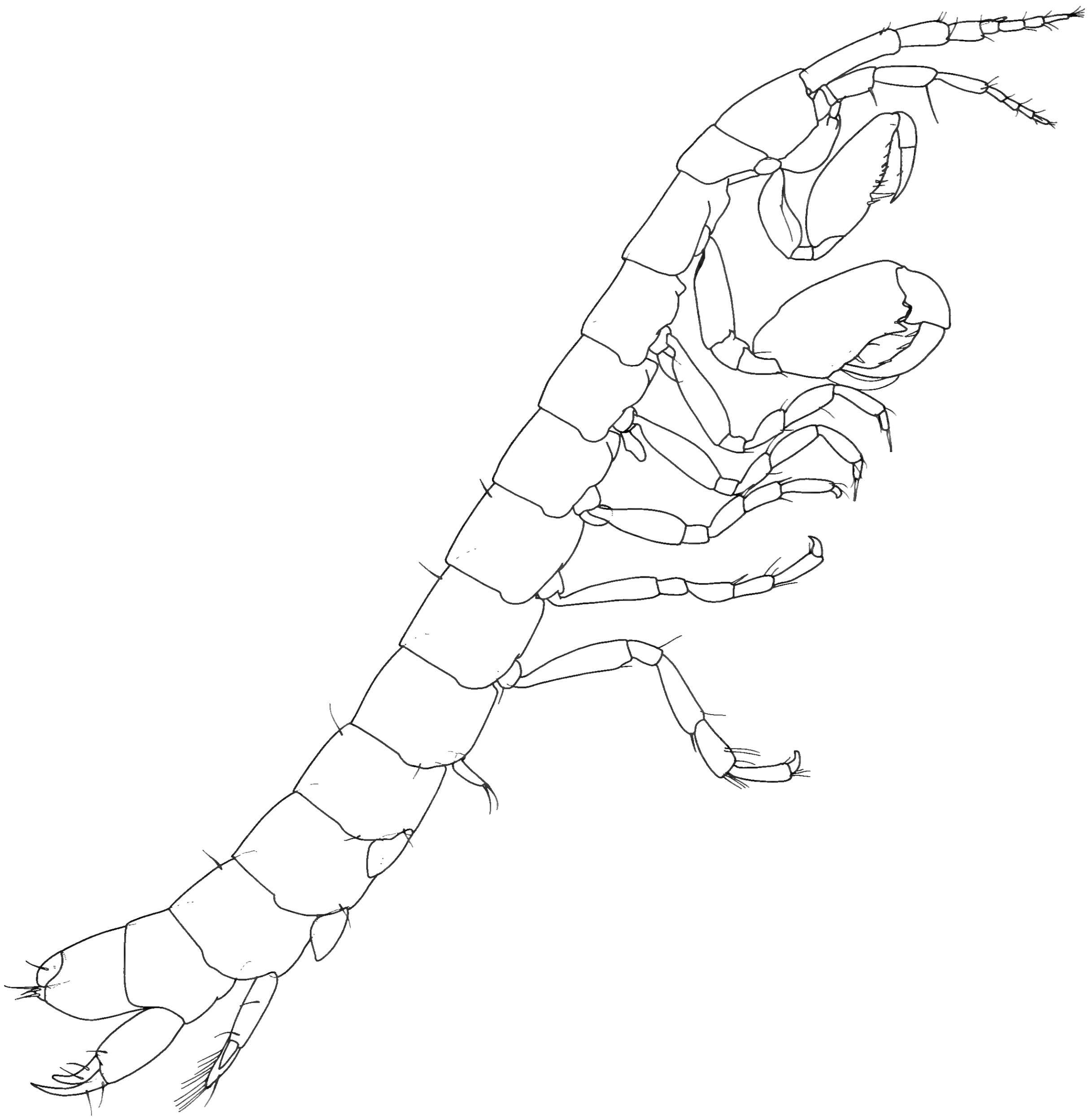

Fig. 1. *Ingolfiella australiana,* holotype male, NMV J12851; southwest of King Island, Bass Strait, Australia. Abbreviations are as follows: A1, A2 = Antennae 1–2; D = Penes; G1, G2 = Gnathopods 1–2; H = Head; LL = Lower lip; l = Left; MD = Mandible; MX1, MX2 = Maxillae 1–2; MP = Maxilliped; P3–P7 = Peraeopods 3–7; PL1–PL3 = Pleopods 1–3; r = Right; T = Telson; U1–U3 = Uropod 1–3; UR3 = Urosomite 3.

Description of holotype.—Body elongate, all segments laterally compressed. Head, anterodorsal margin angular, without rostrum; "eye-lobe" semicircular, small. Peraeonite 1 about half as long as head; posteroventral margin oblique; much deeper anteriorly than posteriorly such that peraeonites 1 and 2 are separated by a waist. Peraeonites 2 to 7 increasing in depth posteriorly. Pleonites 1 to 3 with posteriorly rounded epimera. Urosomites 1 and 2 not markedly differentiated from pleonites, of similar length; urosomite 3 with lateral plates enclosing base of telson and uropod 3.

Antenna 1, peduncular article 1 as long as head; article ratio 1.0:0.4:0.3; flagellum slightly less than half length of peduncle, five articles, last minute; accessory flagellum just longer than article 1 of flagellum, three articles, last minute. Antenna 2, peduncle as long as peduncle of antenna 1; flagellum of five articles, about one-third length of peduncle.

Left mandible, incisor with four teeth; la-

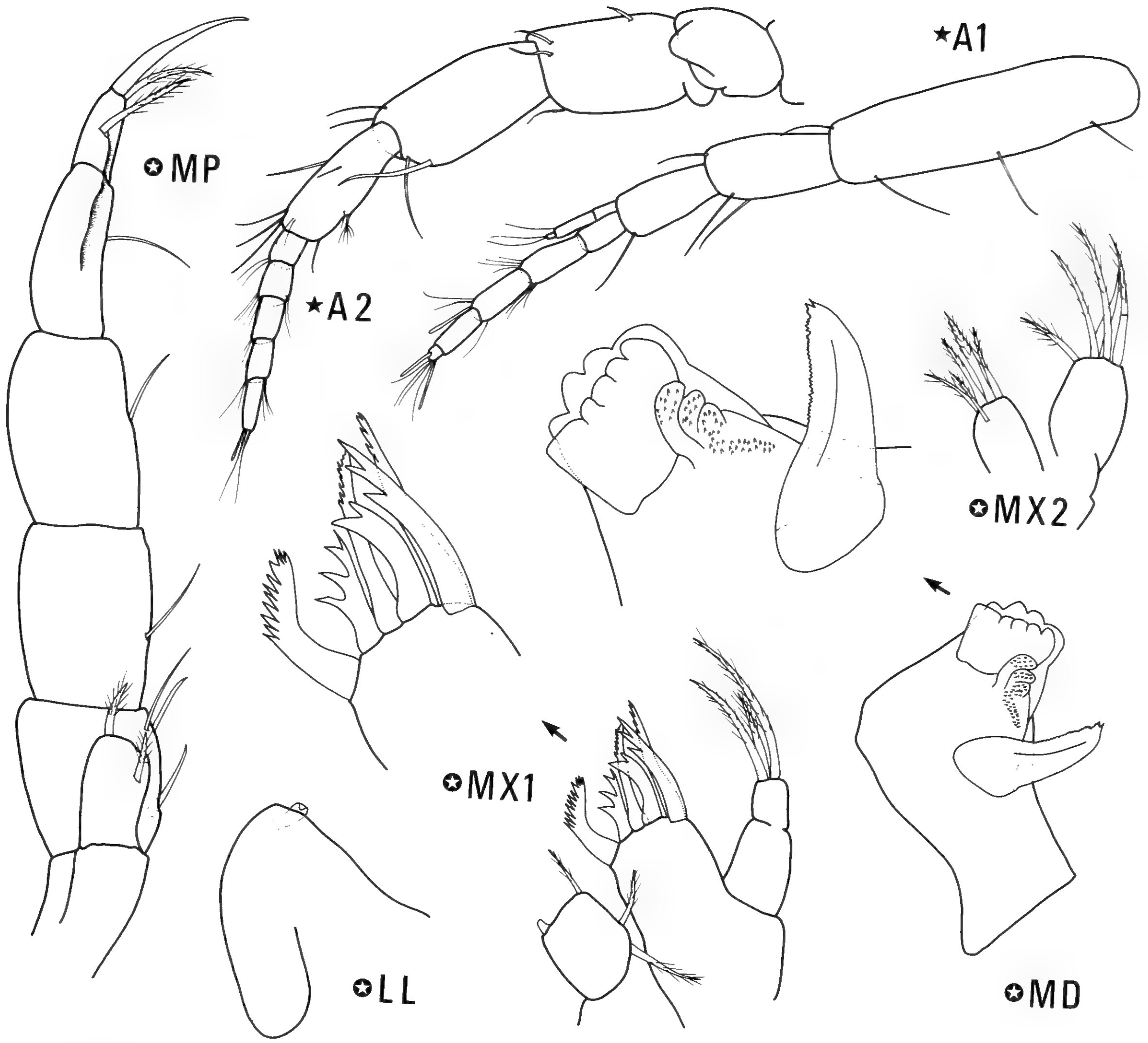

Fig. 2. *Ingolfiella australiana,* holotype male, NMV J12851 (circle star); paratype "female," NMV J12850 (star); southwest of King Island, Bass Strait, Australia. For Abbreviations see Fig. 1.

cinia mobilis as broad as incisor, with five teeth; spine row of three curved, denticulate spines; molar a long triangular blade with minutely denticulate margin. Maxilla 1, inner plate subquadrate, with four setae; outer plate with three strong cuspidate spines in anterior row, two denticulate spines in posterior row, and one well developed curved comb-spine medially; palp of two articles, with three apical plumose setae. Maxilla 2, inner plate with one subterminal seta and four terminal setae; outer plate with five setae. Maxilliped, basal endite with one subapical and one apical seta; palp articles 1 to 4 with three, one, one, and one mesial setae respectively, article 5 with long falcate unguis, seta at midlength and at base of unguis.

Gnathopod 1 carpochelate, palm strongly oblique; coxa inserted at anteroventral corner of peraeonite; carpus 2.2 times as long as wide, palm with three proximal spines and eight setae, without teeth; dactylus with four serrations. Gnathopod 2 carpochelate, palm slightly oblique; carpus 1.6 times as long as wide; palm defined by strong curved spine, distally with triangular tooth and quadrate tooth separated by narrow notch, with one spine and four setae (one seta proximal to definitive palm spine); propodus with two triangular blades posteriorly, distal blade larger; dactylus with three teeth on posterior margin, dactylus longer than palm, extending over carpus.

Peraeopods 3 and 4, dactylus with two distal setae and cylindrical bifid unguis. Peraeopods 5 to 7, basis slightly broadened in

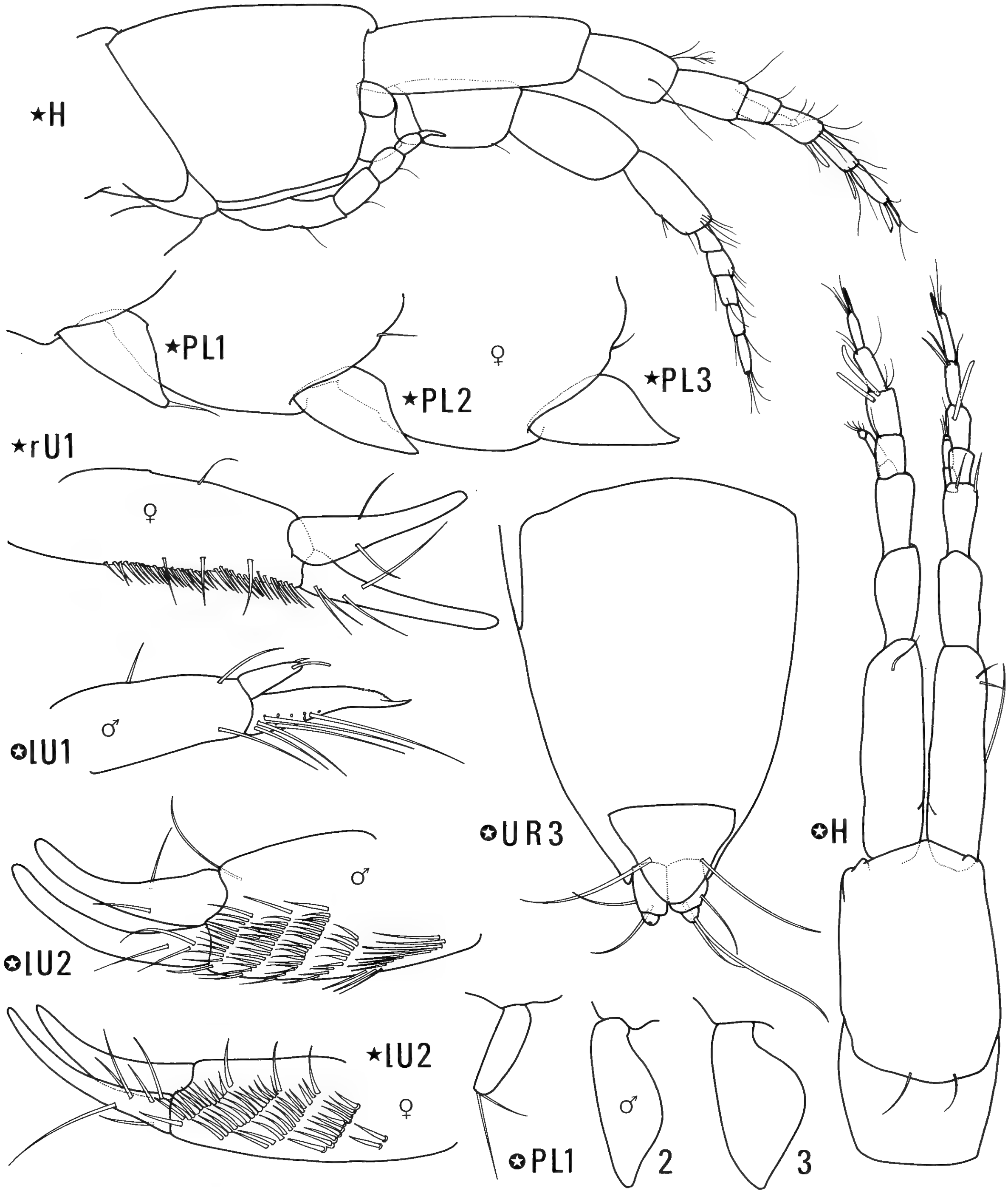

Fig. 3. *Ingolfiella australiana,* holotype male, NMV J12851 (circle star); paratype "female," NMV J12850 (star); southwest of King Island, Bass Strait, Australia. For Abbreviations see Fig. 1.

peraeopod 5, becoming progressively narrower in peraeopods 6 and 7; dactylus stout, curved, unguis not defined.

Pleopod 1 cylindrical with two setae; pleopods 2 and 3 subtriangular.

Uropod 1, peduncle 1.3 times as long as inner ramus; inner ramus with lateral row of 10 long setae, 4 apical spines in dished tip, edges of apex finely denticulate; outer ramus 2.2 times as long as inner ramus, with 2 distal setae. Uropod 2, peduncle with 5 oblique rows of (proximal to distal) 11, 9, 17, 15, 12 spines mesially (2 spines between rows 4 and 5); inner ramus ¾ length of peduncle, with 3 proximal setae; outer ramus shorter than inner with 2 setae near mid-

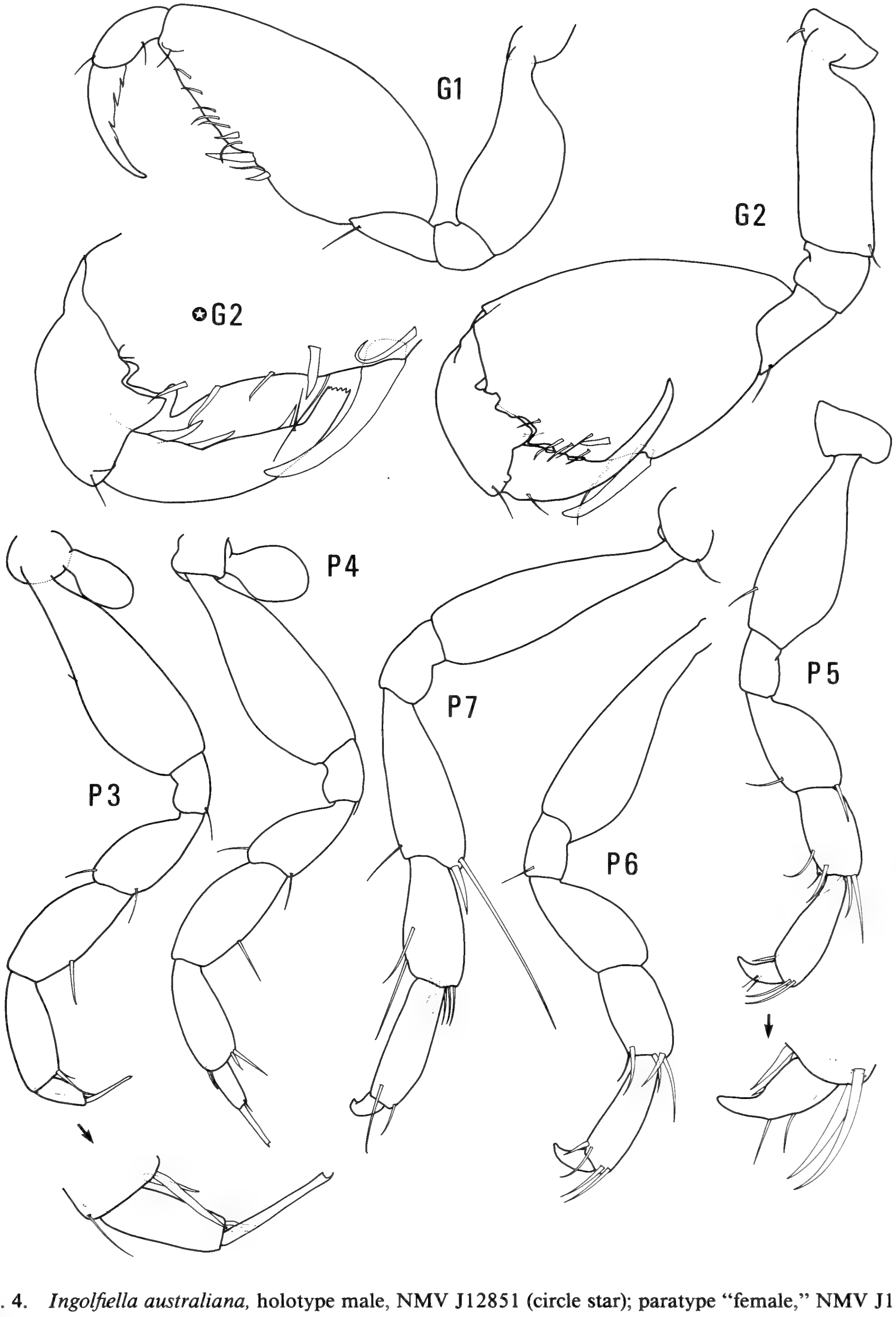

Fig. 4. *Ingolfiella australiana,* holotype male, NMV J12851 (circle star); paratype "female," NMV J12850; southwest of King Island, Bass Strait, Australia. For Abbreviations see Fig. 1.

length. Uropod 3 with one ramus; peduncle with two setae, ramus short, broad, with distal seta. Telson subtriangular, with pair of long dorsal setae.

Variation.—Paratype, 2.2 mm. "Eye-lobe" reaches to article 2 of antenna 2. Gnathopod 2, palm convex, triangular and blade-like teeth poorly defined, with five setae (no seta proximal to definitive palm spine); propodus, teeth blunt. Pleopod 1 subtriangular with one seta. Uropod 1, peduncle 1.6 times as long as inner ramus, with longitudinal-oblique row of four setae, ventrally with a dense brush of stout, short setae; inner ramus with two setae at midpoint; outer ramus longer than inner ramus, with four setae. Uropod 2, peduncle with 5 oblique rows of (proximal to distal) 2, 10, 13, 15, 13 spines mesially.

Etymology.—For Australia.

Remarks.—The holotype of *Ingolfiella australiana* is most similar to the South African species *I.* (*Trianguliella*) *berrisfordi* Ruffo, 1974 and the West Indian species *I.* (*T.*)*grandispina* Stock, 1979. *Ingolfiella berrisfordi* has two setae on the inner plate and five spine-teeth on the outer plate of maxilla 1; pleopod 1 is subtriangular; pleopods 2 and 3 are broader and distally truncate; uropod 1 has a shorter inner ramus; and uropod 2 has a basofacial hook on the peduncle. *Ingolfiella grandispina* has the dactylus and unguis separate on peraeopods 5 to 7; pleopods broad and distally truncate, and a slightly better developed ramus on uropod 3.

Ingolfiella australiana is different from the other three species assigned to *Trianguliella*: *I.* (*T.*) *manni* Noodt, 1961 which has long, slender endites on the maxilliped and three spine-rows on the peduncle of uropod 2; *I.* (*T.*) *macedonica* Karaman, 1959 in which the palmar spine and the dactylus of gnathopod 2 are not enlarged; and *I.* (*T.*) *thibaudi* Coineau, 1968 in which males have only pleopod 1 and females have no pleopods.

Uropod 1 of the paratype of this species is unusual in the possession of a ventral peduncular row of stout setae not reported in any other ingolfiellidean.

Ingolfiella bassiana, new species
Figs. 5–8

Type specimens.—Holotype male, 1.8 mm, NMV J13124 with 2 slides, paratype "female," 1.8 mm, NMV J13119 with 2 slides; 3 paratype males, 1.7 to 1.9 mm J13125, J13126, AM P38458; 6 paratype "females" (without oostegites), 1.1 to 1.8 mm NMV J13120, with 2 slides, to J13123, AM P38459, 75 km WSW of Cape Otway, 39°02.4′S 142°37.8′E, Bass Strait, Australia, 121 m, shelly sand, dredge, G.C.B. Poore on HMAS *Kimbla,* 9 Oct 1980 (NMV station BSS 64).

Description.—Based on holotype, male, 1.8 mm, and paratypes, "females," 1.8 mm, NMV J13119 and 1.7 mm, NMV J13120. Body elongate, all segments laterally compressed. Head, anterodorsal margin rounded, without rostrum; "eye-lobe" semicircular, small. Peraeonite 1 about half as long as head; posteroventral margin oblique; deeper anteriorly than posteriorly such that peraeonites 1 and 2 only weakly separated. Peraeonites 2 to 7 increasing in depth posteriorly. Pleonites 1 to 3 with posteriorly rounded epimera. Urosomites 1 and 2 not markedly differentiated from pleonites, of similar length; urosomite 3 with lateral plates enclosing base of telson and uropod 3.

Antenna 1, peduncular article 1 as long as head; article ratio 1.0:0.4:0.3; flagellum of four articles, slightly less than half length of peduncle; accessory flagellum of two articles, last longer, reaching midlength of article 2 of flagellum. Antenna 2, peduncle as long as peduncle of antenna 1; flagellum of five articles, about one-third length of peduncle.

Mouthparts of juvenile (NMV J13120) (Fig. 6). Left mandible, incisor with three cusps; lacinia mobilis as broad as incisor, with five cusps; spine row of three curved, denticulate spines; molar a long triangular blade with minutely serrate margin. Right

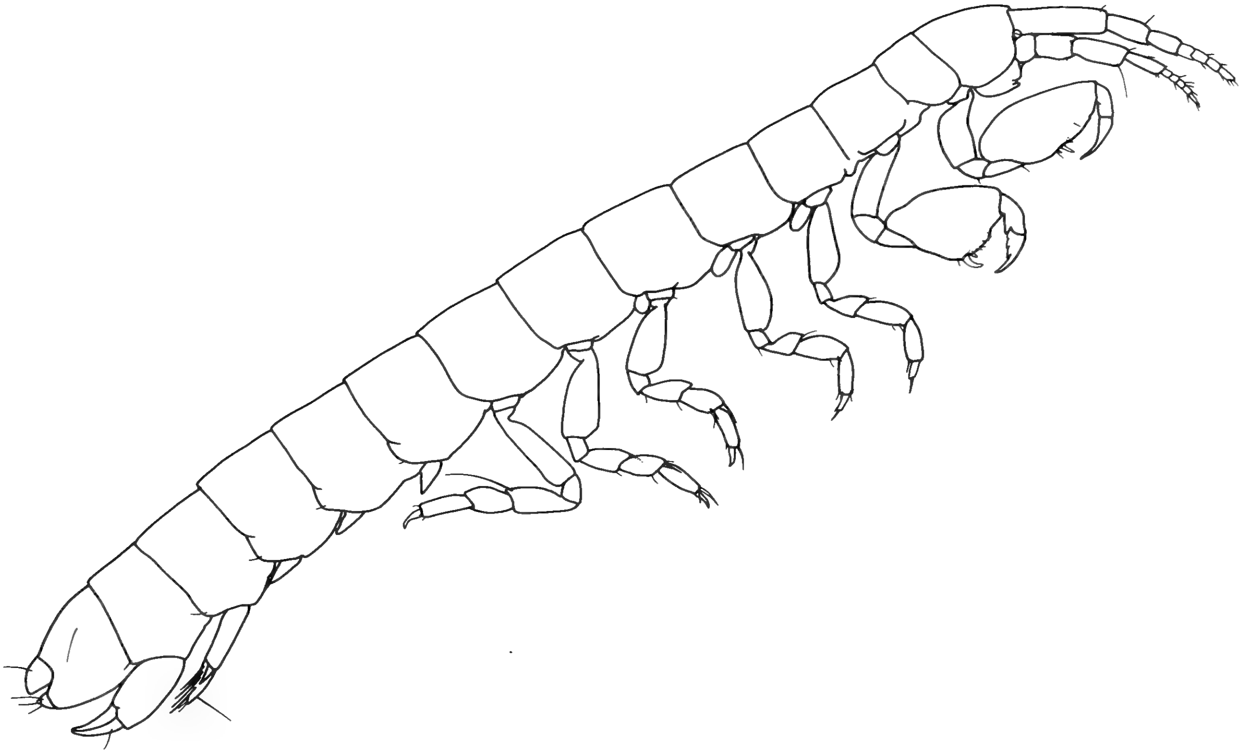

Fig. 5. *Ingolfiella bassiana,* paratype, "female," 1.8 mm, NMV J13119; southwest of Cape Otway, Bass Strait, Australia.

mandible, incisor with four cusps on two overlapping blades; lacinia mobilis almost as broad as incisor with denticulate margin; two denticulate spines, and molar same as left. Maxilla 1, inner plate distorted, with three setae apparent; outer plate with three strong cuspidate spines in anterior row, two denticulate spines in posterior row, and one well developed curved comb-spine mesially; palp of two articles, with one naked and two plumose apical setae. Maxilla 2 unknown. Maxilliped, basal endite with two apical setae; palp articles 1 to 4 with two, one, one, and one mesial setae respectively, article 4 with oblique row of slender setae, article 5 with long falcate unguis, seta at midlength and distally.

Gnathopod 1 carpochelate, palm oblique; coxa at anterior of peraeonite; carpus 2.2 times as long as wide, palm with three proximal spines, three weaker spines and three setae, without teeth; dactylus with three spines along posterior margin. Gnathopod 2 carpochelate, palm nearly transverse; carpus 1.6 times as long as wide; palm defined by one reversed pectinate seta and three strong complex spines, (mesial spine complexly bifurcate, two lateral spines simpler), palm obliquely transverse, with a triangular tooth at midlength, with three stout setae and two finer setae laterally and three setae mesially, propodus with a triangular blade posteriorly; dactylus with three teeth on inner margin; dactylus as long as palm, not extending over carpus.

Peraeopods 3 and 4, dactylus with two distal setae and cylindrical bifid unguis. Peraeopods 5 to 7 becoming narrower posteriorly; dactylus stout, curved, unguis not defined.

Pleopods subtriangular, with notch on oblique margin; pleopods 1 and 2 each with two terminal setae.

Uropod 1, peduncle 1.4 times as long as inner ramus with lateral, plumose setae; inner ramus with a mesial row of four long setae and four distal spines; outer ramus 0.6 times as long as inner ramus, with one seta. Uropod 2, peduncle with proximoventral hook and 4 obliquely transverse rows of

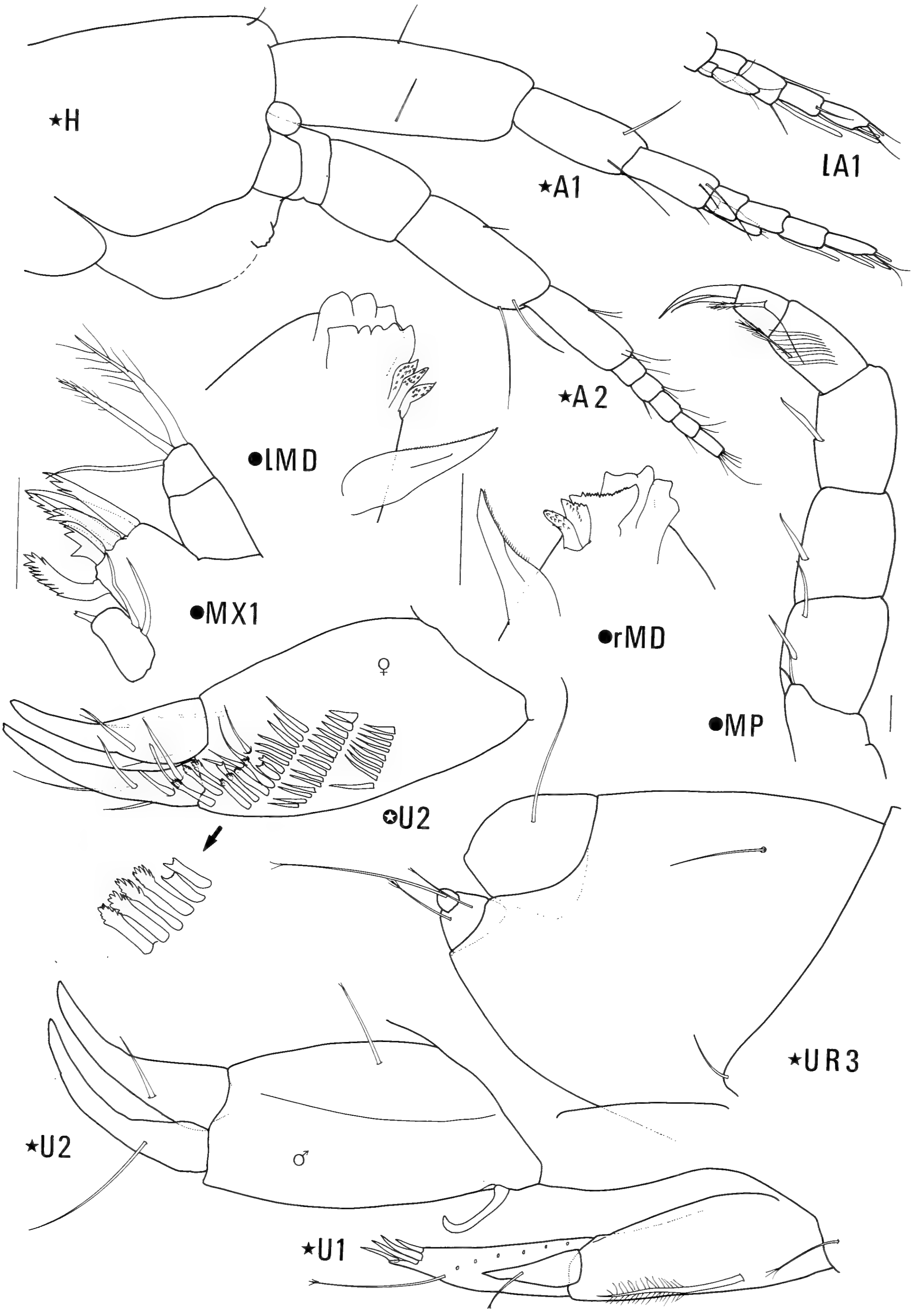

Fig. 6. *Ingolfiella bassiana,* holotype, male, 1.8 mm, NMV J13124 (closed star); paratype, "female," 1.7 mm, NMV J13120 (closed circle); paratype, "female," 1.8 mm, NMV J13119 (circle star); southwest of Cape Otway, Bass Strait, Australia. For Abbreviations see Fig. 1.

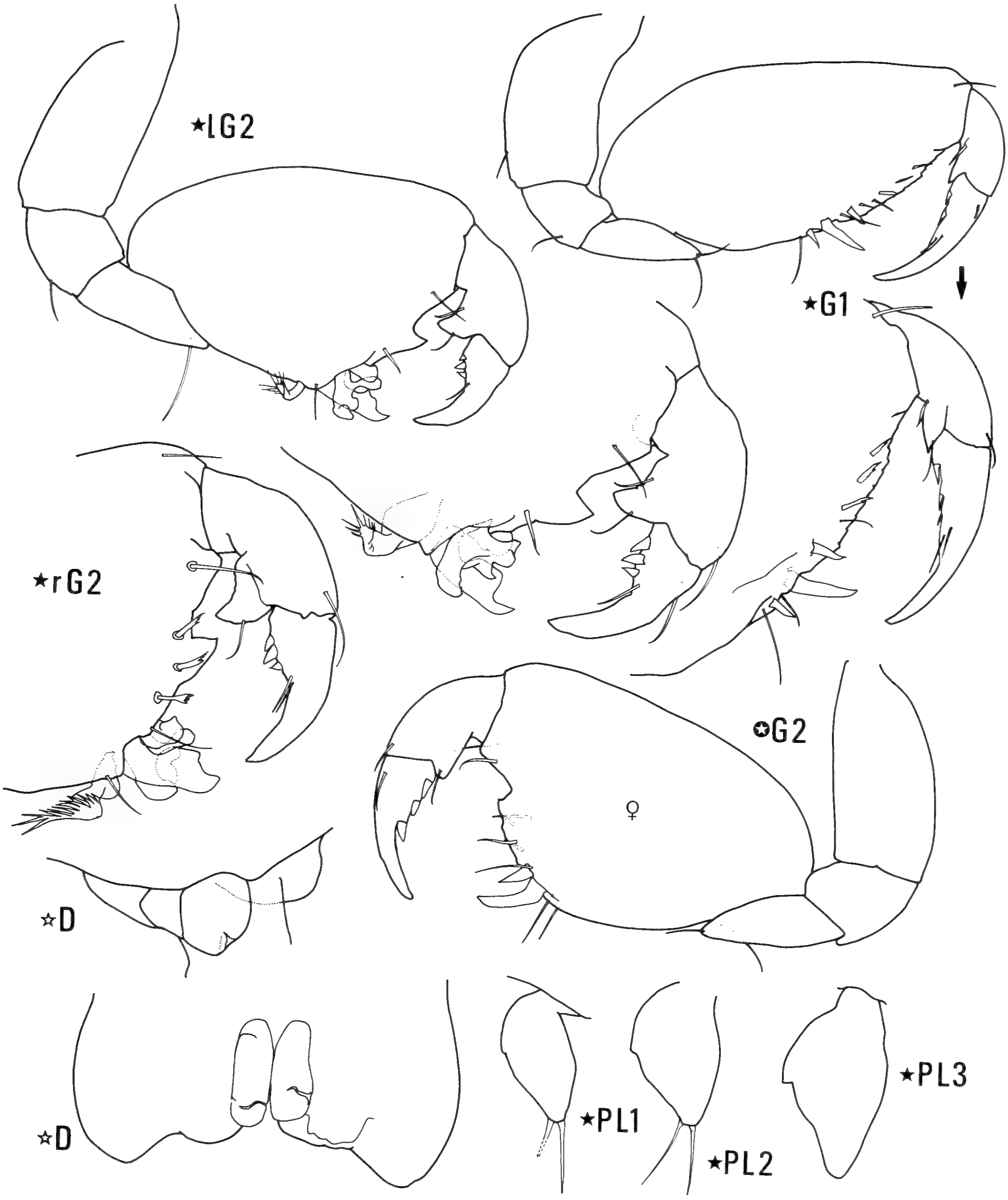

Fig. 7. *Ingolfiella bassiana,* holotype, male, 1.8 mm, NMV J13124 (closed star); paratype "female," 1.8 mm NMV J13119 (circle star); paratype, male, 1.8 mm, NMV J13125 (open star); southwest of Cape Otway, Bass Strait, Australia. For Abbreviations see Fig. 1.

(proximal to distal) 12, 16, 13, 8 spines (those ventrally in third and fourth rows apically complex); rami 1-articulate, equal, 0.6 times length of peduncle, inner ramus with 4 setae; outer ramus with transverse row of 3 spines plus 3 setae. Uropod 3 with one ramus; peduncle with two lateral setae, ramus short, broad, with long distal seta. Telson subtriangular, with pair of long dorsal setae.

"*Females.*"—As in male but: gnathopod 2 carpus palm defined by two spines, palm oblique and with distal notch; propodus with straight posterior margin; dactylus with three

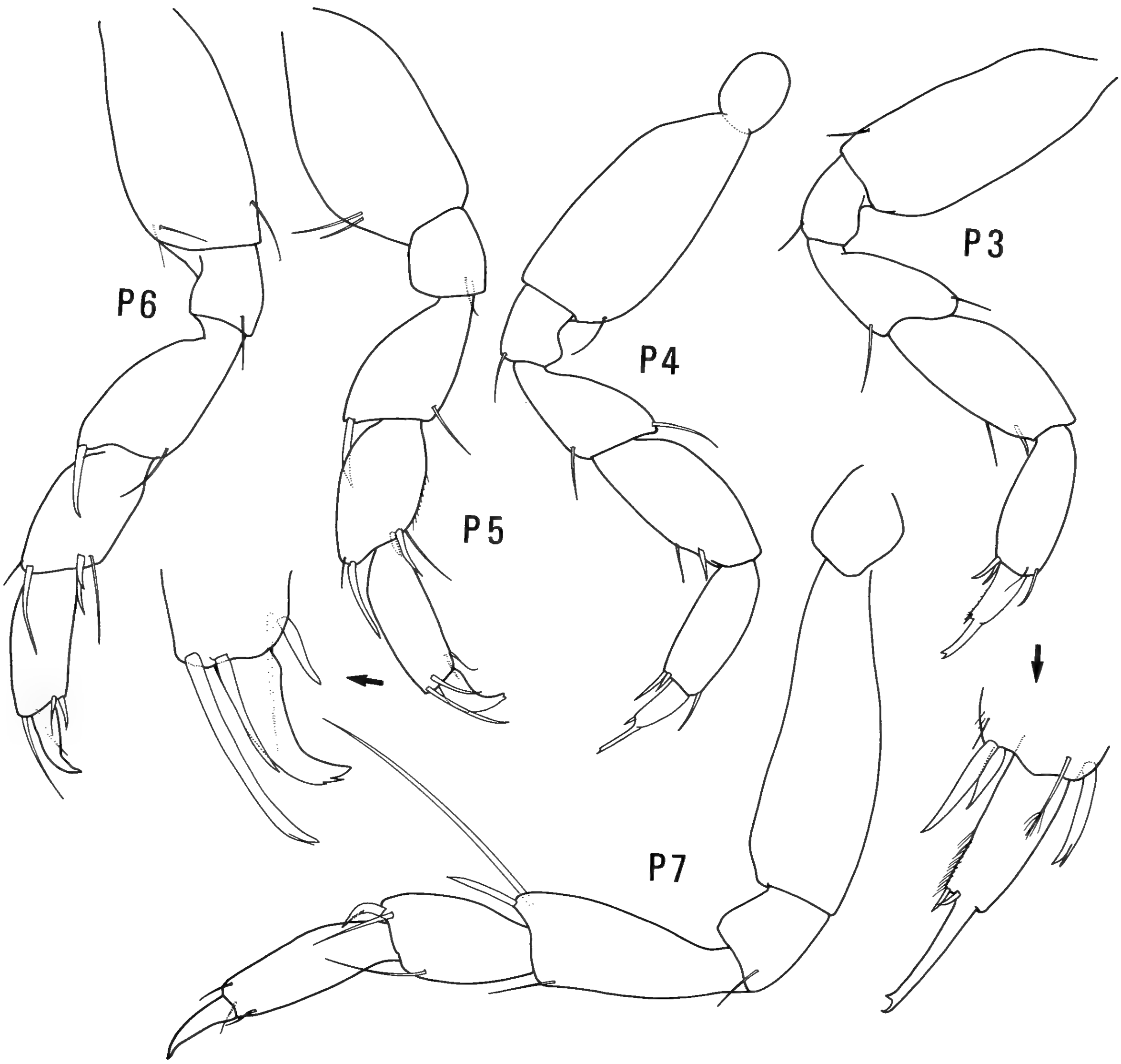

Fig. 8. *Ingolfiella bassiana,* holotype, male, 1.8 mm, NMV J13119; southwest of Cape Otway, Bass Strait, Australia. For Abbreviations see Fig. 1.

oblique proximal teeth. Pleopods without distal setae. Uropod 1 peduncle without lateral plumose seta. Uropod 2 peduncle without proximoventral hook, with 4 mesial transverse rows of (proximal to distal) 9, 15, 12, 8 spines.

Etymology.—For Bass Strait.

Remarks.—The possession of triangular pleopods and a basofacial hook on uropod 2 allies *I. bassiana* to the five West Indian and Canary Islands species in the subgenus *Gevgeliella* discussed by Ronde-Broekhuizen & Stock (1987). All differ from the type species *I. petkovskii* Karaman, 1957, and the two other Mediterranean species of *Gevgeliella* (*I. catalanensis* Coineau, 1963 and *I. vandeli* Bou, 1970) which do not have these characters. The complexity of the palmar spines on male gnathopod 2 and apical setae on pleopods 1 and 2 distinguish *I. bassiana* from all of these species.

Stock (1979) has suggested that the reversed seta on gnathopod 1, the apical setae on pleopod 1 and the basofacial hook on uropod 2 are all male characters of *Gevgeliella*. Our holotype has all of these characters and paired penial processes. Our "female" specimens do not, thus confirming Stock's presumptions.

The complex nature of the mesial spines on uropod 2 (shown here in female) have been illustrated (for *I. fuscina*) previously only by Dojiri and Sieg (1987). Males of *I. bassiana* possess a long plumose seta on the peduncle of uropod 1, a character never before reported.

Discussion

Sexual dimorphism and subgenera.—Sexual dimorphism was used to help define two of the five subgenera recognized by Stock (1976). It was not used to define the three other subgenera because the data were, and still are, not available. In the absence of information about sexual dimorphism, differences between some subgenera are unconvincing (for example, between *Ingolfiella* and *Hansenliella*). Dojiri & Sieg (1987) also questioned the value of subgenera for the same reason. Stock (1976) used only two dimorphic characters, gnathopod 2 and pleopod 1. We have examined 8 characters which show sexual dimorphism, and surveyed the literature for 25 species. For about half of these species males are not known or cannot be distinguished within the available material. Most of these species fall into subgenera for which sexually dimorphic characters are not considered to be diagnostic.

Some characters are unique or not widely distributed and thus of little phylogenetic value. These apomorphic forms include:

1. Complex palmar spines in the male gnathopod 2 (only *I. bassiana*);
2. Loss of pleopods 2 and 3 in males and 1 to 3 in females (only *I. thibaudi* Coineau, 1968 and *I. catalanensis* Coineau, 1963, Ruffo, pers. comm);
3. Complex distal seta on the peduncle of male uropod 1 (in *I. fuscina* Dojiri & Sieg, 1987 and *Trogloleleupia eggerti* Ruffo, 1951);
4. Row of stout ventral setae in "female" uropod 1 (only *I. bassiana*).

Other characters are more widespread and may indicate phylogenetic affinities. These include:

5. Reversed seta on carpus of gnathopod 2 (occurs in all species assigned to *Gevgeliella* and *Trogloleleupia eggerti*);
6. Male pleopod 1 digitiform (most species of *Trianguliella* and *G. catalanensis*;
7. Male apical setae on pleopod 1 (all species for which males are known);
8. Uropod 2 with male peduncular basofacial hook (most, but not all species of *Gevgeliella, I. bassiana, Trianguliella berrisfordi* and *Trogloleleupia eggerti*).

Among the widespread sexually dimorphic characters there is overlap between genera and subgenera and the existing arrangement is not well supported by this investigation. Until more males are known and more species are discovered subgeneric classification within the Ingolfiellidae is unstable.

It is probable that some form of sexual dimorphism is plesiomorphic in ingolfiellideans (Dojiri and Sieg 1987). When the plesiomorphic type is established and the derived types are understood, then these forms may be used to define species groups.

Subordinal status.—Recently Bowman & Abele (1982), based on the extensive arguments of Dahl (1977), abandoned the suborder Ingolfiellidea and placed both of its families in the suborder Gammaridea. Dahl looked at several characters from earlier works by Hansen (1903), Ruffo (1951), and Siewing (1963). He concluded that of these characters only the "eye-lobe" could be used to define the group at the subordinal level.

The presence of an "eye-lobe" in ingolfiellideans was first noted by Hansen (1903). Dahl (1977) seemed unconvinced that this structure, a small scale on the side of the head of some species, is a rudimentary stalked eye. He noted: "Its functional significance is unknown, and it contains no dioptric and apparently also no nervous elements. Its location, however, corresponds well with that of the lobate rudiment of the compound eye in *Gammarus*. . ." Bowman (1984), citing Dahl, was equally equivocal: "Whether these lobes represent eyestalks is questionable."

Only three of seven peracaridan orders contain species with unambiguous eyestalks. In the Mysidacea (numerous species) the eyestalks carry well developed terminal eyes. In the Spelaeogriphacea, where only two living species are known (*Spelaeogriphus lepidops* and *Potiicoara brasiliensis*), the lobe has no pigment or optic structure (Gordon 1957, Pires 1987). In Mictacea one of the three species known (*Mictocaris halope*) has pyriform eyestalks lacking visual elements (Bowman & Iliffe 1985). In the only pancaridan order, four of the six Thermosbaenacea genera have plate-like eyestalks but lack pigment (Bowman & Iliffe 1986, 1988). Eyestalks in the syncarid family Anaspididae are similar to those in peracaridans. The spelaeogriphaceans, the thermosbaenaceans and the mictacean are troglobitic so it is not surprising that they are blind. What is notable is that the eyestalks in all these groups attach obliquely above the first antenna near the base of the rostrum, a position and attitude very different from that of the ingolfiellidean scale.

It seems probable that the hinged ingolfiellidean "eye-lobe" is the anterolateral margin of the head, often produced at this point in amphipods, whether it bears a sessile eye or not. A similar situation is seen in the tanaidacean genus *Heterotanais* in which the eyes occur on hinged lobes (Sars 1896). These are in the same position, ventral to the antennae, as the normally sessile eyes of other tanaidaceans.

We think that the so-called "eye-lobe" of ingolfiellideans is not homologous to that of other peracaridans or of other malacostracans. The "eye-lobe" therefore is not of subordinal importance.

Dahl (1977) did not take into account the single species of the second ingolfiellidean family, *Metaingolfiella mirabilis* (Ruffo, 1969). The plesiomorphic characters of this species provide further evidence for the placement of the group within the Gammaridea. The pleopods of *M. mirabilis* are biramous, typical of most Gammaridea, and quite unlike the reduced form of the Ingolfiellidae. On peraeopods 3 and 4 the unguis is undifferentiated, as in Gammaridea, and not specialized as in Ingolfiellidae. The mandibular molar is a fixed process, not articulating as in Ingolfiellidae. The existence of *Metaingolfiella* removes any argument for retaining a separate suborder.

Relationships within the Gammaridea.—Many of the unusual characters of the ingolfiellideans are associated with their interstitial way of life and are paralleled by other crustaceans in similar habitats. The maxilliped, gnathopods 1 and 2, and the telson may help place the group within the Gammaridea.

In considering the polarity of character states in the following discussion we have use the isopods for outgroup comparison. Most peracaridan groups, including the isopods, have a maxilliped with a basal endite and a palp of five articles, a condition which we consider plesiomorphic among peracaridans. This state also occurs in ingolfiellideans and in all members of the gammaridean families Cressidae, Leucothoidae, Pagetinidae, Stenothoidae and Thaumatelsonidae. This is in contrast to the more widely held view that a maxilliped with both basal and ischial endites (the usual gammaridean state) is plesiomorphic (Bousfield 1979). The small ischial endite which occurs in some of these families is thus a developing rather than a reducing condition.

Carpochelate gnathopods are an important character defining the ingolfiellideans. A similar condition is known in leucothoids, some corophioids, the deep sea pardaliscid *Eperopeus abyssicola* Mills, 1967, and is widespread among the hyperiideans. There can be little doubt that carpochely has arisen more than once, but the leucothoids are the only group which share the primitive maxilliped with the ingolfiellideans.

The telson is entire in all peracaridan groups. The only exception is some Amphipoda. We consider it to be the plesiomorphic condition among the isopods and the amphipods. It is entire in the ingolfiellideans, leucothoids, corophioids and representatives within other families. We recognize that within the Amphipoda the entire telson has been secondarily derived many times. This contrasts with the view of Bousfield (1979) that the laminate cleft telson is plesiomorphic.

The evidence for phylogenetic relationships of the ingolfiellideans within the Gammaridea is meager. The ingolfiellideans and the leucothoids are the only living amphipods without an ischial endite on the maxilliped. This is the usual form in all other peracaridans, and indicates that the evolution of ischial endites occurred after the amphipods arose as a distinct group. The ingolfiellideans and the leucothoids both have carpochelate gnathopods. These observations may be interpreted as a phylogenetic link between the ingolfiellideans and the leucothoids and may indicate that both groups were derived early and close from the amphipodan stem.

Acknowledgments

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ALLOCRANGONYCTIDAE AND PSEUDOCRANGONYCTIDAE, TWO NEW FAMILIES OF HOLARCTIC SUBTERRANEAN AMPHIPOD CRUSTACEANS (GAMMARIDEA), WITH COMMENTS ON THEIR PHYLOGENETIC AND ZOOGEOGRAPHIC RELATIONSHIPS

John R. Holsinger

Abstract.—Two new families of gammaridean amphipod crustaceans, Allocrangonyctidae and Pseudocrangonyctidae, are described. The former is composed of a single genus that occurs in south-central United States; the latter is composed of two genera that occur in northeastern Asia. Members of both families inhabit subterranean freshwaters and are of stygobiont facies. Although the phylogenetic relationship of the allocrangonyctids is unclear, they are apparently allied with the genus *Pseudoniphargus* and may be aberrant hadzioids. The pseudocrangonyctids are allied with the Holarctic family Crangonyctidae and are assigned to the superfamily Crangonyctoidea.

The North American amphipod genus *Allocrangonyx* Schellenberg, and the east Asian genera *Pseudocrangonyx* Akatsuka & Komai and *Procrangonyx* Schellenberg were originally assigned to the *Crangonyx* group of the old family Gammaridae (s.l.) by Schellenberg (1936). In recent years, however, the Gammaridae have been split into a number of separate families, and many of the genera placed in the *Crangonyx* group by Schellenberg have been assigned to different families. Some of these genera are now placed in the family Crangonyctidae (see Holsinger 1977, 1986a, b), with which *Allocrangonyx, Pseudocrangonyx* and *Procrangonyx* have sometimes been associated (see Bousfield 1983, Holsinger 1986a, b). Although these genera may be somewhat "crangonyctid-like" in overall similarity, they possess unique character state combinations that preclude their membership in this family (see Holsinger 1986a, b). Both *Allocrangonyx* and *Pseudocrangonyx/Procrangonyx* have been referred to informally as separate family groups by several workers (Bousfield 1977, 1978, 1982; Holsinger 1977, 1986b), but heretofore neither group has been given formal family status. In this paper, I will show that each group represents a distinct family of gammaridean amphipods. Their phylogenetic, zoogeographic and super-familial relationships will also be examined.

Allocrangonyctidae, new family

Type genus (and only known genus).—*Allocrangonyx* Schellenberg, 1936.

Diagnosis.—Without eyes or pigment, of stygobiont facies. Body smooth except for few dorsal spines on uronites. Sexually mature male larger than female, with sexually dimorphic uropod 3. Interantennal lobe of head rounded anteriorly, inferior antennal sinus shallow. Antenna 1 longer than 2, accessory flagellum 2-segmented. Antennae lacking calceoli. Mandibles well developed; left lacinia mobilis 4-dentate; molar triturative; palp 3-segmented. Lower lip with thick inner lobes. Inner plate of maxilla 1 with one apical seta, outer plate with eight or nine unmodified (non-serrate/pectinate) apical spines. Apical margin of outer plate of maxilla 2 uneven (weakly bilobed), with two distinct sets of unequal setae; inner plate without oblique row of facial setae. Inner plate of maxilliped short, much smaller than outer; inner margin of outer plate with row of bladelike spines.

Coxae 1–4 rather shallow, posterior margin of 4 weakly excavate. Propods of gnathopods powerful, subchelate, 2nd nearly twice size of 1st; palms bearing double row of tiny spines, many distally notched. Carpus (segment 5) of gnathopod 1 subequal in length to propod, that of gnathopod 2 proportionately much shorter. Pereopods 5–7 increasing in length posteriorly but otherwise generally similar; dactyls of 6 and 7 with several sets of anterior and posterior marginal spines. Coxal gill of gnathopod 2 large and bilobed; coxal gills of pereopods 3–6 ovate or subovate, with very short (rudimentary) stalks. Sternal gills absent. Brood plates sublinear. Distoposterior corners of pleonal plates not acuminate. Pleopods subequally biramous. Uronite 3 without ecdysial spine on ventral margin. Margins and apices of uropods 1 and 2 with spines, peduncle of 1 with basofacial spine. Uropod 3 elongate, biramous (parviramous); inner ramus greatly reduced (scale-like); outer ramus well developed, bearing tiny 2nd segment, becoming greatly elongate and secondarily segmented in larger males. Telson short, with shallow apical notch, apical lobes with spines.

Relationship.—In comparison with a number of potentially related outgroups of gammaridean amphipods, including the Crangonyctidae, Hadziidae, Niphargidae, Pseudocrangonyctidae (new family described below), and *Pseudoniphargus* (probable family group, but not formally named to date), the Allocrangonyctidae possess at least five, presumably autapomorphic, character states that, in full combination, make them unique: (1) large, bilobed coxal gill on gnathopod 2; (2) non-serrate (or non-pectinate) spines on apex of outer plate of maxilla 1; (3) stalks of coxal gills vestigial; (4) posterior marginal spines on dactyls of pereopods 6 and 7; and (5) positive allometric growth in combination with secondary segmentation of outer ramus of male uropod 3.

Although the allocrangonyctids share a number of important characters with other genera, such as *Pseudoniphargus, Niphargus,* and members of the Crangonyctidae (see Holsinger 1971, Bousfield 1977, Barnard & Karaman 1980, Notenboom 1988), their phylogenetic relationship has never been clearly demonstrated. *Allocrangonyx* shares at least 14 apomorphic characters with the peri-Mediterranean, amphi-Atlantic subterranean genus *Pseudoniphargus* Chevreux (and its satellite genus *Parapseudoniphargus* Notenboom) (Table 1). At least seven of these characters are also shared with the western Palearctic subterranean genus *Niphargus* (characters 1, 3, 4, 6, 7, 10, 13) but there are also a number of important differences between this genus and *Allocrangonyx* (see Holsinger 1971, Notenboom 1988). In addition, five of these characters are shared with genera in the Holarctic family Crangonyctidae (characters 1, 8, 11, 13, 14), but character 8 of the crangonyctids may be different (i.e., the palmar spines are proportionately much larger), and character 11 is variable among species in several genera. Based on the significantly greater number of apomorphic characters shared by *Allocrangonyx* and *Pseudoniphargus*, the allocrangonyctids are obviously more closely related phylogenetically to the latter than they are to either *Niphargus* or the crangonyctid genera.

Allocrangonyx Schellenberg

Allocrangonyx Schellenberg, 1936:33 (type species by original designation, *Niphargus pellucidus* Mackin, 1935).—Holsinger, 1971:318-319.—Barnard & Barnard, 1983:447–448.

Remarks.—Many of the important characters of the genus are clearly stated in the literature (see above) and need not be repeated here. Some omissions and mistakes in earlier descriptions should be pointed out, however. Segment 3 of the mandibular palp is heavily setose and bears A, B, C, D and E setae. Carpus of gnathopod 1 is relatively long, approximately as long as the propod; merus bears a small, semihyaline posterior lobe. Carpus of gnathopod 2 is short, less than ½ the length of propod, and bears a distinct (narrow) posterior lobe. A majority of palmar margin spines on the gnathopods in the outer row are distally notched and not simply "spinate" or setule tipped as indicated by Holsinger (1971). Coxal gills (on pereopods 3–6) have vestigial peduncles or stalks. Coxal gill 1 shown by Barnard & Barnard (1983:211, fig 9I) is mislabelled a sternal gill. The small basofacial spine on peduncle of uropod 1 was inadvertently omitted on plate 107 (fig. 4m) in Holsinger (1971) and also in the diagnosis by Barnard & Barnard (1983:448). Uropod 3 of the male shown in Holsinger (1986a:540, fig. 1) is drawn too short; it should be about twice as long as indicated.

At present the genus is composed of two troglobitic species from south-central United States, the geographic distributions of which are shown on a number of range maps (see Holsinger 1971, Barnard & Barnard 1983, Holsinger 1986a, b). The distributions shown in Holsinger (1986b, fig. 6) encompass all known localities recorded to date, including those given below.

Allocrangonyx pellucidus (Mackin)
Fig. 1

Allocrangonyx pellucidus (Mackin).—Holsinger, 1971:320–322 (with references).—Black, 1971:7.—Holsinger, 1972:77, fig. 32b.—Black, 1973:15.—Reisen, 1975:28, 30.—Pennak, 1978:460, fig. 317H, K.—Barnard & Barnard, 1983:447–448, fig. 18D—Fitzpatrick, 1983:151.—Holsinger, 1986a:540, 542, fig. 1; 1986b:97.

Range.—Caves and springs of the Arbuckle Mountains in south-central Oklahoma (Murray and Pontotoc counties).

Table 1.—List of 14 apomorphic character states shared by *Allocrangonyx* and *Pseudoniphargus/Parapseudoniphargus*. Outgroups used to determine character polarity include: Crangonyctidae, Gammaridae, Hadziidae, Niphargidae and Pseudocrangonyctidae.

1. Accessory flagellum of first antennae 2-segmented.
2. Lacinia mobilis of left mandible 4-dentate.
3. Lower lip with thick inner lobes.
4. Apical setae of inner plate of maxilla 1 reduced in number (typically less than 3) and often non-plumose, or only weakly so.
5. Apical margin of outer plate of maxilla 2 uneven and bearing two distinct groups of setae.
6. Inner plate of maxilla 2 without oblique row of facial setae.
7. Inner plate of maxilliped reduced in size relative to outer plate.
8. Distally notched spines on palms of gnathopod propods.
9. Merus of gnathopod 1 with posterior lobe (sometimes semihyaline, sometimes pubescent).
10. Absence of sternal gills.
11. Brood plates narrowly sublinear.
12. Peduncle of uropod 1 with basofacial spine.
13. Inner ramus of uropod 3 reduced to scalelike plate.
14. Telson relatively short and not deeply notched or cleft (lobes nearly completely fused).

New locality record (since Holsinger 1971) based on material in author's collection.—Oklahoma, Murray County: spring on Honey Creek near Davis (W. K. Reisen, collector).

Allocrangonyx hubrichti Holsinger
Figs. 2, 3

Allocrangonyx hubrichti Holsinger, 1971: 324–326, pls. 107–109 (with references).—Holsinger, 1972:77–78, fig. 32a.—Pflieger, 1974:36.—Craig, 1975:4; 1977:83.—Nordstrom et al., 1977:8.—Barnard & Barnard, 1983:447–448, fig. 9I.—Fitzpatrick, 1983:151.—Wilson, 1984:26.—Gardner, 1986:17–18.—Holsinger, 1986a:542; 1986b:97.

Range.—Caves and spring(s) of the Ozark Plateau in east-central Missouri (Phelps, Pulaski and Washington counties).

New locality records (since Holsinger

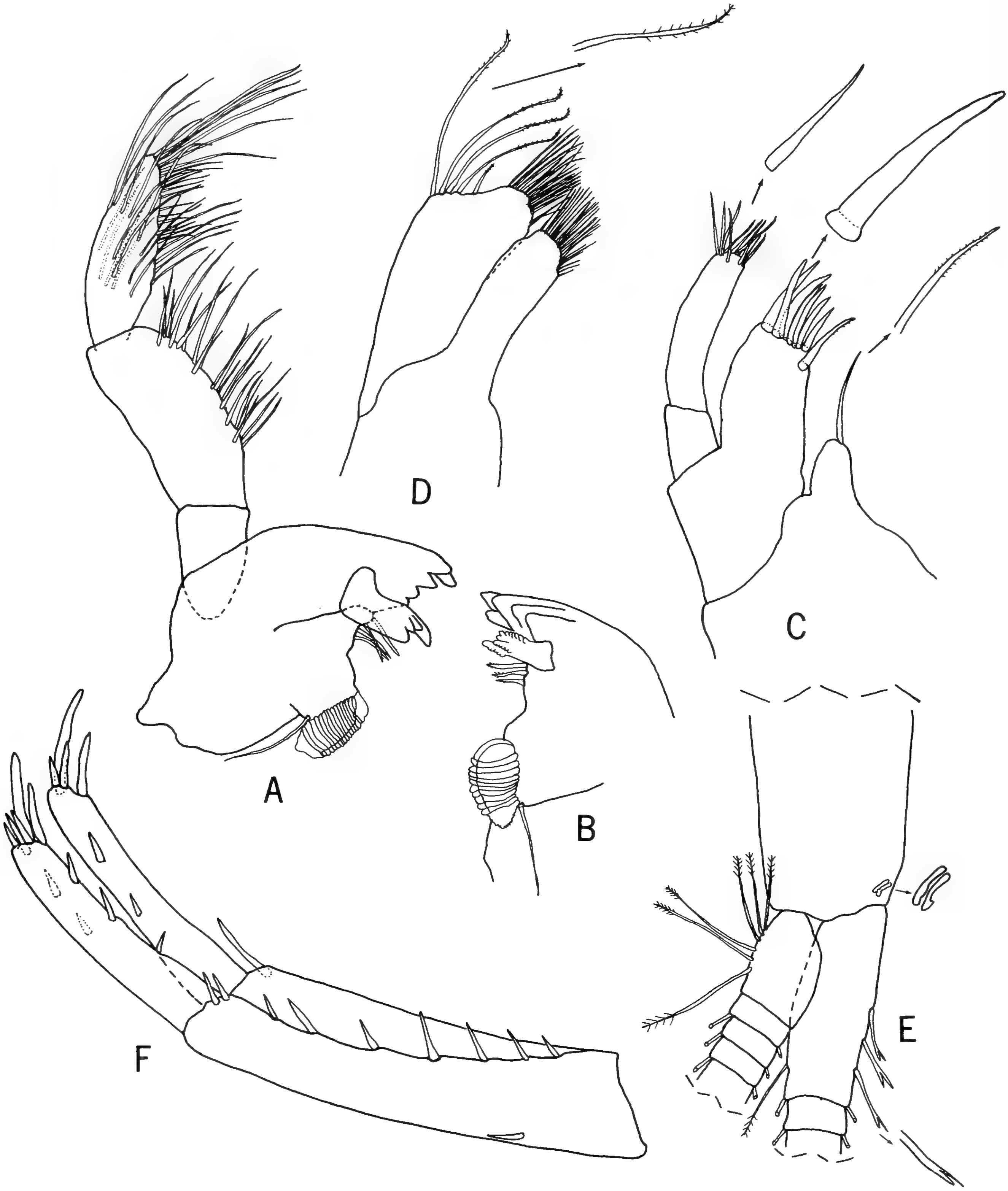

Fig. 1. *Allocrangonyx pellucidus* (Mackin). Male (21.75 mm), seep, 0.5 km NW of Turner Falls, Murray County, Oklahoma: A, Left mandible; B, Dentate part of right mandible; C, Maxilla 1; D, Maxilla 2. Maxillae drawn to larger scale than mandibles. Female (18.00 mm) from same locality: E, Pleopod 1 (in part), F, Uropod 1.

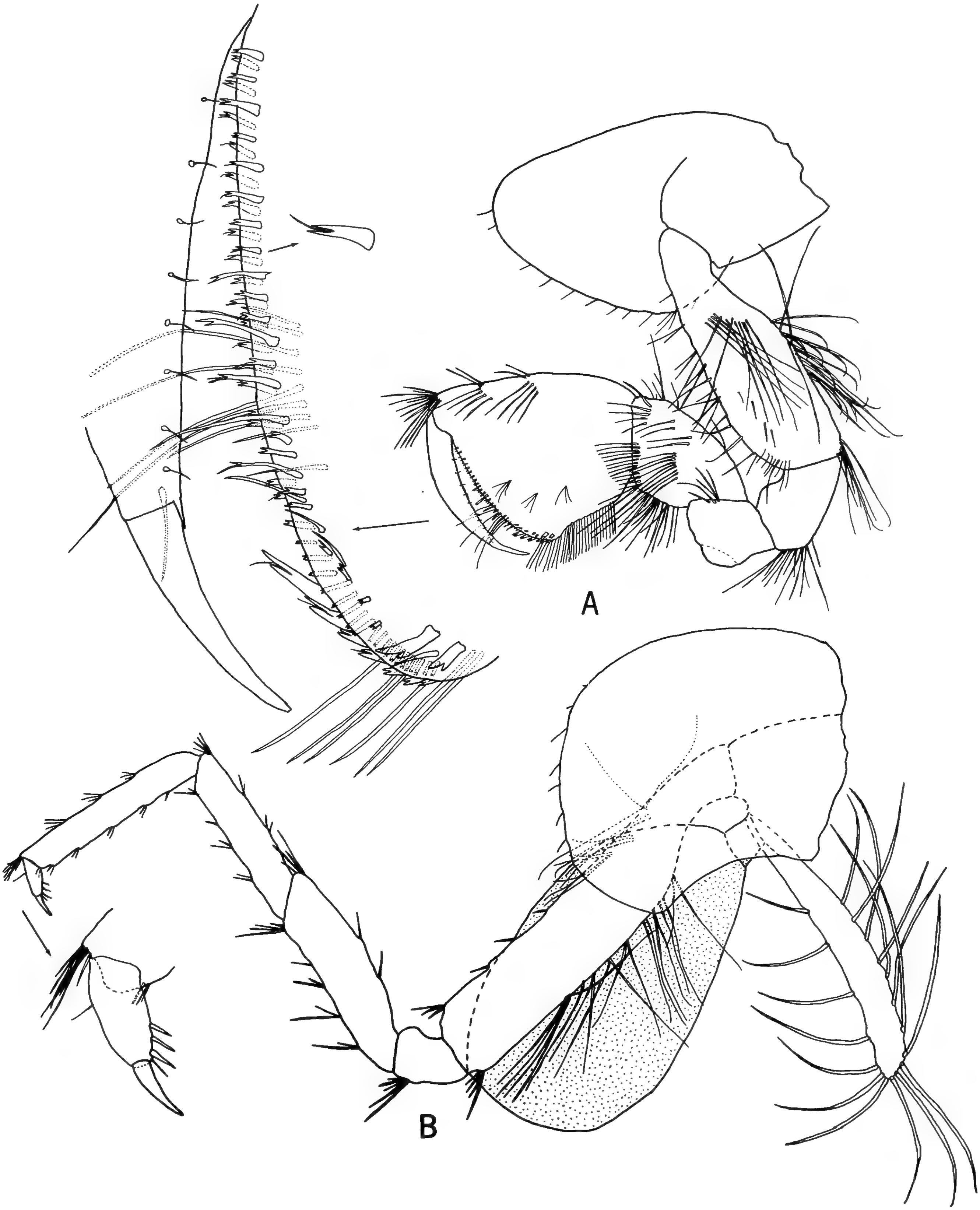

Fig. 2. *Allocrangonyx hubrichti* Holsinger. Female (17.00 mm), Saltpeter Cave, Phelps County, Missouri: A, Gnathopod 1 (palm enlarged); B, Pereopod 4 (dactyl enlarged). Gnathopod and pereopod drawn to same scale.

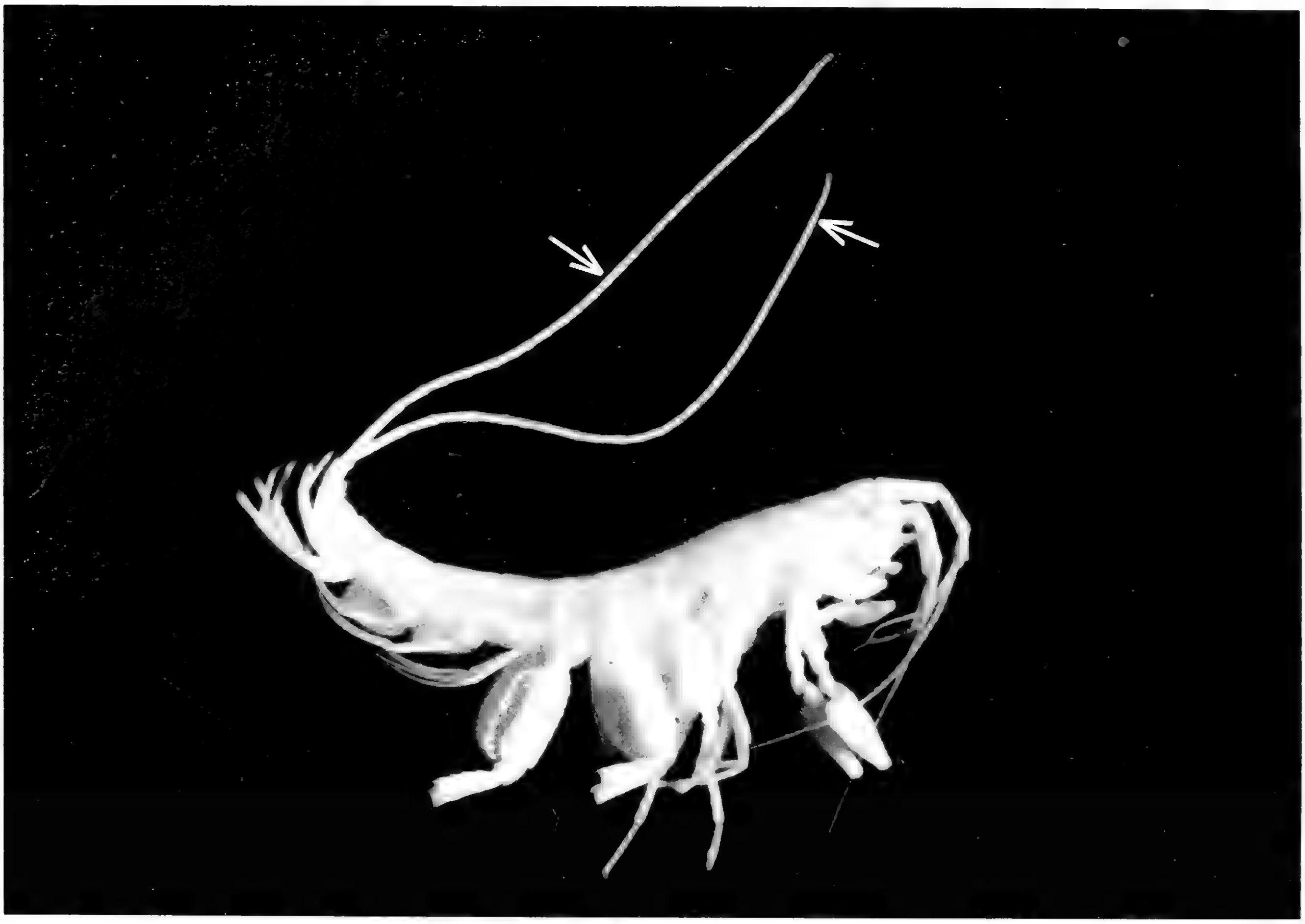

Fig. 3. Male specimen (16.0 mm) of *Allocrangonyx hubrichti* Holsinger from Kaintuck Hollow Natural Bridge, Phelps County, Missouri. Elongate 3rd uropods indicated by white arrows. Note that last three segments of pereopods 6 and 7 are broken off.

1971); based on material in author's collection).—Missouri, Phelps County: Kaintuck Hollow Natural Bridge (in stream pool), 18 km SW of Rolla (J. E. Gardner, coll.).—Meramec Spring, 8 km SE of St. James (J. E. Gardner, coll.). Pulaski County: Killam Cave (in pool), 14 km S of Waynesville (J. E. Gardner, coll.). Washington County: Hamilton Springs Cave (in pool), 12 km SE of Sullivan (J. L. Craig and T. Cravens, coll.).—Mossy Spring Cave (in stream), 16 km E of Richwoods (J. E. Gardner, coll.).

Remarks.—The remarkable developmental changes in the third uropod of both species of *Allocrangonyx* were discussed at some length by Holsinger (1971). During growth, the second segment of the outer ramus decreases in proportion to an increase in size of the first segment in both sexes. In males, the first segment of the outer ramus increases allometrically in relation to both the length of the peduncle and the body and, in concert with increase in size, the outer ramus differentiates into secondary segments. This unusual secondary sexual dimorphism is even more pronounced in *A. hubrichti.* For example, as reported earlier (Holsinger 1971, 1972) uropod 3 was 45% as long as the body, with 9 secondary segments, in a 15.0 mm-long male, and 65% as long as the body, with 16 secondary segments, in a 18.0 mm-long male. In a more recently collected male specimen, 16.0 mm in length, uropod 3 was as long (or slightly longer) than the body, with 30 secondary segments (see Fig. 3).

Elongation of uropod 3 in larger males of many species *Pseudoniphargus* has also been reported (Stock 1980). But in this genus, the peduncle may also become elongate and the outer ramus neither differentiates into secondary segments nor reaches the extraordinary length seen in *A. hubrichti* (Stock 1980, Notenboom 1986, 1988). Although there are no observations on the reproductive behavior of these organisms, the possibility that the hyperextended third uropod of the male of *Allocrangonyx* is utilized either in sex recognition or manipulation of the female during copulation, or even agonistic behavior between males, should be investigated.

Pseudocrangonyctidae, new family

Type genus.—*Pseudocrangonyx* Akatsuka & Komai, 1922.

Diagnosis.—Typically without eyes (except one species) and pigment, of stygobiont facies. Body generally smooth, except last seven body segments bearing dorsal setae and uronite 2 bearing few small dorsal spines. Sexually mature females larger than males. Interantennal lobe rounded anteriorly, inferior antennal sinus shallow. Antennae 1 longer than 2, accessory flagellum 2-segmented. Antennae without calceoli. Apical margin of upper lip rounded, unnotched. Mandibles well developed; molar weakly triturative, bearing single seta or not; left lacinia mobilis 5-dentate; segment 3 of palp equal in length to segment 2, with A (sometimes), D and E setae. Inner lobes of lower lip small or vestigial. Inner plate of maxilla 1 with apical plumose setae, outer plate with typically seven serrate (or pectinate) spines. Inner plate of maxilla 2 with oblique row of facial setae. Inner margin of outer plate of maxilliped with setae and few small spines, but lacking bladespines.

Coxae shallow, barely touching or typically discontiguous; posterior margin of 4 without excavation. Propods of gnathopods relatively large (crangonyctid-like), subchelate; propod of 1 a little larger than 2; palms rather long, oblique, armed with double row of distally notched spines (possibly variable). Carpus of gnathopod 1 short, with small posterior lobe; that of 2 longer, without lobe. Pereopods 3 and 4 normal, subequal in length. Pereopods 5–7 increasing in overall length posteriorly; bases with small distoposterior lobes. Stalked coxal gills on gnathopod 2 and pereopods 3–6. Single median sternal gills on pereonites 2–4 or 2–5. Brood plates small, sublinear. Distoposterior corners of pleonal plates not acuminate. Pleopods normal, subequally biramous; peduncles with 2 coupling spines each. Uropods 1 and 2 biramous, with marginal and apical spines; peduncle of 1 with basofacial spine(s). Uropod 3 uniramous; ramus elongate, bearing spines and few setae, 2nd segment present and short, or absent. Telson longer than broad; apical margin with notch of variable depth but typically rather shallow (not deeper the ½ length of telson); apical lobes with few spines.

Remarks.—At present this family is composed of two northeast Asian genera, *Pseudocrangonyx* and *Procrangonyx.* Their geographic distribution is shown on maps in Barnard & Barnard (1983) and Holsinger (1986b). Unfortunately, previous descriptions of taxa assigned to this family have been very uneven. Thus important taxonomic details are available for some species (e.g., *Pseudocrangonyx asiaticus* and *P. coreanus*) but are lacking or unclear for others (e.g., *Procrangonyx* and other species of *Pseudocrangonyx*). It may therefore be necessary to amend the family diagnosis given above as these missing taxonomic details become available.

Relationship.—Although the Pseudocrangonyctidae are allied with the Holarctic family Crangonyctidae as indicated below, they differ from this group in a number of important characters and warrant recognition as a distinct family: (1) segment 3 of mandibular palp equal in length to segment 2; (2) molar of mandible weakly triturative (or perhaps not triturative in some species); (3) gnathopods and pereopods tending to be more setose, especially segment 2 (basis) of the gnathopods and pereopods 3 and 4, and the coxae of pereopods 5–7; (4) coxae generally discontiguous (a character shared with many members of the family Bogidiellidae); (5) abdominal segments (pleonites and uronites) and 7th pereonite with clusters of setae dorsodistally; (6) uronites with small spines (1st with ecdysial spine on ventral margin, 2nd with few dorsodistal spines, 3rd with several spines ventrodistally near base of peduncle of uropod 3); and (7) uropod 3 uniramous and elongate, with ramus 3 to 6 times length of peduncle.

A relatively close phylogenetic relationship between the families Pseudocrangonyctidae and Crangonyctidae is indicated by similarity of the following characters, most of which are apparently synapomorphies: (1) 2-segmented accessory flagellum; (2) structure of mouthparts, except that mandibular palp segment 3 is proportionately a little longer and the molar is not as strongly developed in the Pseudocrangonyctidae (see above); (3) similar shape of, and proportionately large, gnathopod propods (in combination with short carpi); (4) palms of gnathopod propods with double row of thick, distally notched spine teeth (although possibly variable in Pseudocrangonyctidae); (5) rastellate setae on carpus of one or both gnathopods; (6) median sternal gills; (7) loss of inner ramus of uropod 3 (cf. *Stygobromus* and *Synurella*); and (8) relatively short telson with shallow apical notch (variable).

Pseudocrangonyx Akatsuka & Komai

Pseudocrangonyx Akatsuka & Komai, 1922: 120 (type species not designated therein).—Uéno, 1966:504–505 (with references).—Barnard & Barnard, 1983:442–443 (type species *Pseudocrangonyx shikokunis* Akatsuka & Komai, designated therein).

Remarks.—Nine species are included in this genus at present; detailed range maps are found in Birstein (1955), Uéno (1966) and Barnard & Barnard (1983). They inhabit subterranean waters (e.g., caves, springs, wells) in northeastern China, eastern Siberia (including the Kamchatka Peninsula), Korea and the Japanese Islands (see Holsinger 1986a). Further details on one of these species are given below.

Pseudocrangonyx asiaticus Uéno
Fig. 4

Pseudocrangonyx asiaticus Uéno.—Uéno,1966:506–518, figs. 2–8 (with references); 1971:198.—Barnard & Barnard, 1983:443, figs. 8B, 9G, 11B, 18C, 20A.—Holsinger, 1986a:542, fig. 4.

Material examined.—South Korea: Gosugul (cave), 2 males collected by B. A. Lee (in Zoölogisch Museum of Amsterdam collection); Simbog-gul (cave) (location in Uéno 1966:502–503), 12 females, 6 males, 1 juv. collected by K. S. Lee (in author's collection).

Range.—Subterranean waters in Korea, northeastern China and the Tsushima Islands of Japan.

Remarks.—Although Uéno's (1966) redescription of this species (and also the description of *P. coreanus* in the same paper) was very thorough, my recent examination of the above material revealed some taxonomic details that were either omitted or should be further emphasized as follows.

Segment 3 of mandibular palp equal in length to segment 2, bearing several short A setae on outer margin, row of short D setae on distal half of inner margin, and 7 to 8 longish E setae of unequal length on apex. Mandible: molar weakly triturative, bearing 1 seta; left lacinia mobilis 5-dentate. Dactyls of gnathopods with row of bladelike processes (spines?) on inner margin; ungues relatively long. Propod of gnathopod 1: palm with uneven double row of distally notched spine teeth and row of long setae on outside; medial setae present, in sets of 2s and 4s. Propod of gnathopod 2: palm with double row of 5 distally notched spine teeth; defining angle with 2 spine teeth on

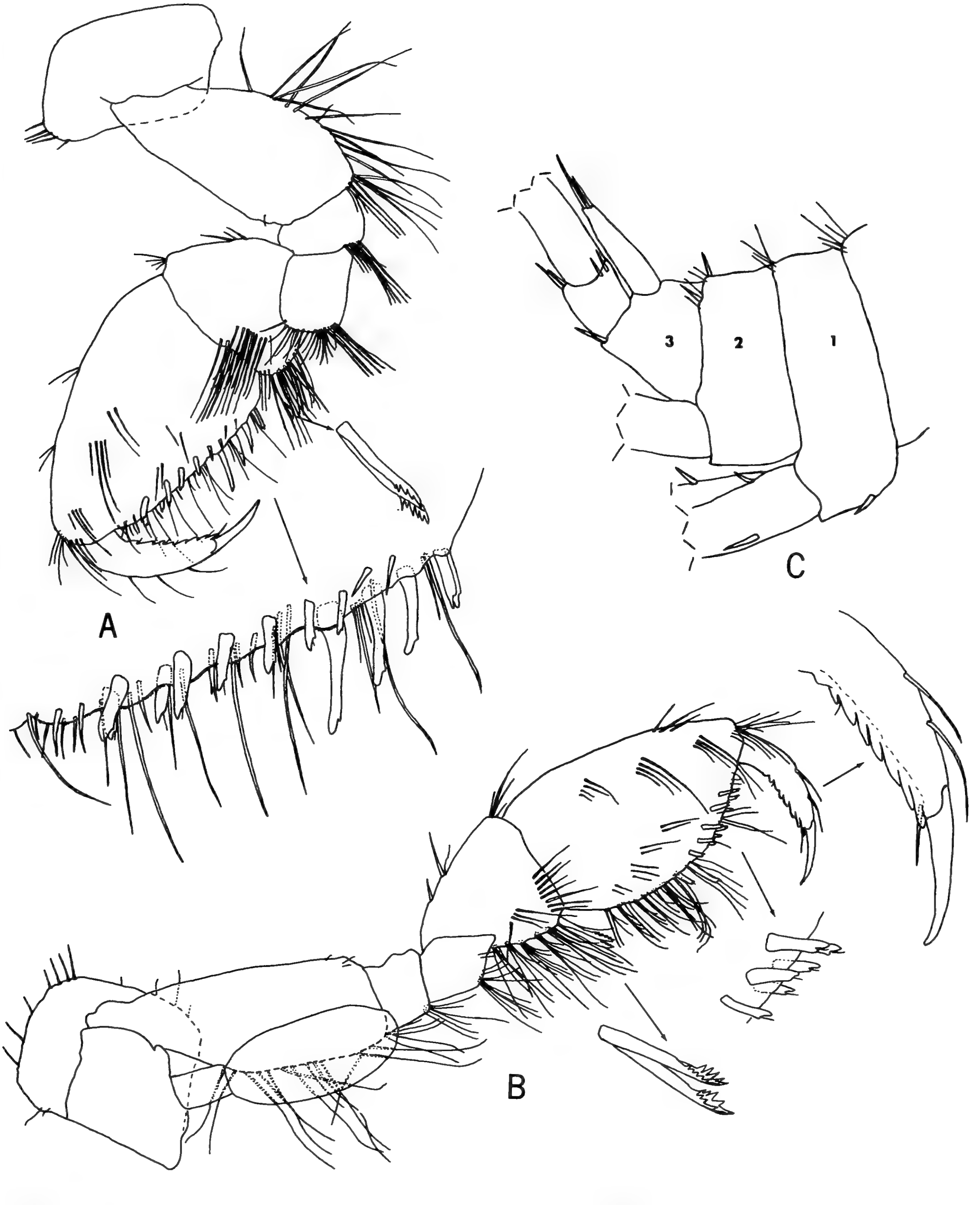

Fig. 4. *Pseudocrangonyx asiaticus* Uéno. Female (10.2 mm), Simbog-gul (cave), South Korea: A, Gnathopod 1 (rastellate setae and palmar margin enlarged); B, Gnathopod 2 (dactyl, palmar spines and rastellate setae enlarged). Male (6.9 mm) from same locality: C, Urosome (uronites 1, 2, 3) (Gnathopods and urosome drawn to same scale.)

outside; inferior medial setae in sets of mostly 2s, superior medial setae in sets of 4s. Segment 5 of gnathopods bearing 2 rastellate setae on posterior margin at distal end. Pereonites 5–7 with sternal blisters (small ventral humps) (cf., *Sternophysinx* from South Africa and species of the *hubbsi* group of *Stygobromus* from western United States). Upper half of posterior margins of pleonites (of larger specimens) with short row of fine setae. Pereonite 7 and abdominal segments each with cluster of 4 to 8 fine setae dorsodistally. Uronite 1 with ecdysial spine(s) on ventral margin, uronite 2 with 2 short spines dorsodistally, uronite 3 with few spines ventrodistally near base of peduncle of uropod 3. Uropod 2 of male sexually dimorphic: inner ramus with 2 or 3 distally serrate, apical spines in cluster with several unmodified spines (sexually mature females lack modified apical spines).

Procrangonyx Schellenberg

Procrangonyx Schellenberg, 1934:217 (type species by monotypy, *Eucrangonyx japonicus* Uéno, 1930).—Barnard & Barnard, 1983:444–445.

Eocrangonyx Schellenberg, 1936:37 (objective junior synonym).

Remarks.—*Procrangonyx* is based on a single species, *P. japonicus,* which was described by Uéno (1930) from two male specimens taken from a subterranean stream in the suburbs of Tokyo (see also Holsinger 1977, 1986a). Except for the absence of a 2nd segment on the ramus of uropod 3, this genus appears to be closely allied with *Pseudocrangonyx.* However, Uéno's original description was incomplete, and several important taxonomic details were omitted or are unclear. For example, it cannot be determined from the description whether the palmar margin spines of the gnathopod propods are distally notched or not.

Although Uéno (1930) stated that the type specimens were deposited in the collection of the Otsu Hydrobiological Station, my attempts to borrow this material or further study have been unsuccessful. Unfortunately, there is a good possibility that the type specimens no longer exist.

Discussion

Both mosaic evolution and convergence are common phenomena in the Amphipoda and have resulted in many taxa that are difficult to interpret phylogenetically or to classify with any degree of certainty. Numerous taxa display mosaic patterns, resulting from differential rates of evolution and reflected in curious mixtures of plesiomorphic and apomorphic characters. In many instances a single taxonomically important structure, such as the gnathopod or uropod 3, may display a combination of both primitive and advanced character states. Convergence has led to the evolution of homoplastic structures in taxa that otherwise are apparently only distantly related. Frequently, these homoplasies involve lost or reduced structures (e.g., one or both rami of uropod 3) that are often difficult to interpret cladistically. For these reasons there has been considerable confusion regarding the phylogenetic relationship of the allocrangonyctids with other families of gammaridean amphipods, as well as their placement in a superfamily that most clearly reflects their taxonomic affinities. It is doubtful if morphology alone can ever provide a wholly satisfactory solution to this problem.

Because of their morphological similarity and potential relationship to *Niphargus, Allocrangonyx* and *Pseudoniphargus* were originally aligned in a single, unnamed family group and assigned to the superfamily Niphargoidea by Bousfield (1977, 1978). Barnard & Karaman (1980:13), however, suggested that these two genera "only have in common a few coincidental characters" and therefore should not be assigned to the same family group. They also strongly advocated abandoning the superfamily Niphargoidea and suggested placing both *Pseudoniphargus* and the niphargids in the superfamily Hadzioidea. Subsequently, Bousfield (1982) reassigned *Allocrangonyx* to the superfamily Crangonyctoidea and also suggested that *Pseudoniphargus* is more closely allied to the superfamily Melitoidea (=Hadzioidea). In their treatise "Freshwater Amphipoda of the World," Barnard & Barnard (1983) referred to the "allocrangonyctids" as a member of their "Sternobranchiate Groups (Crangonyctoids)," but they did not propose any formal taxonomic designation.

Despite significant differences in geographic distribution and ecology, which are pointed out below, the allocrangonyctids are probably more closely related phylogenetically to the pseudoniphargids than to any other group of amphipods. Although several workers, including Stock (1980), Barnard & Karaman (1980), and Notenboom (1988), attribute much of the similarity between these two groups to convergence (homoplasy) or as being overvalued, I believe that the high number of apomorphic characters they share suggests otherwise. It is unlikely that so many detailed similarities in the mouthparts and gnathopods of these genera would have resulted from convergence.

The geographic distribution of *Allocrangonyx* is restricted to subterranean freshwaters in the central interior of North America and is far removed from coastal areas at present. Its range does not extend into areas exposed to marine embayments in the Tertiary or even the Cretaceous, but a part of it in southern Oklahoma would have been less than 100 kilometers from marine embayments in the Late Cretaceous (Holsinger 1971). This distribution pattern suggests that *Allocrangonyx* represents a relict lineage, long removed from marine ancestors. In contrast, species of *Pseudoniphargus* occupy a wide range of marine to fresh water, subterranean habitats in the circum-Mediterranean region of southern Europe and North Africa and on several islands in the Atlantic, including the Azores, Madeira and Bermuda (Stock 1980; Stock et al. 1986; Notenboom 1986, 1987a, b, 1988). These species occur at present in coastal areas or in areas that were directly exposed to marine embayments in the Tertiary.

Neither the difference in geographic distribution between *Allocrangonyx* and *Pseudoniphargus,* nor the fact that some species of the latter live in brackish (or even marine) water, rule out the origin of these two groups from a common ancestor, however. The many synapomorphies between these groups indicate a common ancestry. On this basis, I suggest that the allocrangonyctid and pseudoniphargid lineages could have been derived from a widespread ancestor that inhabited the old Tethyan seaway in Mesozoic times. At that time the areas presently occupied by these groups would have been much closer geographically. Subsequent continental movements combined with widening of the Atlantic, regression of shallow inland seas, and various other geological changes would have severely isolated these groups from each other. Divergence during the long period of geographic isolation that followed has produced some major morphological differences, but enough important similarities remain to support an obvious phylogenetic relationship.

Notenboom (1988) has recently pointed out a number of important similarities, presumably synapomorphies, between *Pseudoniphargus* and the monotypic genus *Allomelita,* which occurs in brackish waters and sometimes in interstitial habitats along the coast of Europe from Norway to Portugal. *Allomelita,* in turn, is closely allied with *Melita* and is thus a bona fide member of the superfamily Hadzioidea as presently understood. The cladistic relationship between *Allocrangonyx* and *Pseudoniphargus*-is certainly as strong as that of the latter with *Allomelita,* suggesting, ipso facto, that both the allocrangonyctids and pseudoniphargids may also be members of the Hadzioidea. Although some problems regarding the phylogenetic affinities of *Allocrangonyx* and *Pseudoniphargus* remain unresolved, there is a good possibility that both are highly divergent hadzioids. Their morphological character combinations make it highly improbable that either is a crangonyctoid or niphargoid as some workers have previously suggested.

The phylogenetic relationship of the family Pseudocrangonyctidae is less problematic. The number of apomorphies shared by this family and the Crangonyctidae suggest a relatively close phylogenetic relationship of these two groups. These two families, in turn, can be placed in the superfamily Crangonyctoidea, which by definition also includes the freshwater families Neoniphargidae and Paramelitidae of the Southern Hemisphere (see Bousfield 1978, 1982, 1983; Holsinger 1986a, b; Williams & Barnard 1988).

Both the pseudocrangonyctids and crangonyctids are known only from freshwater habitats in the Northern Hemisphere and lack close morphological affinities with any group of marine amphipods. They are therefore believed to represent very old groups of freshwater amphipods that originated on the Laurasian paleocontinent prior to the separation of Eurasia and North America (Holsinger 1986a, b). Geographically, the pseudocrangonyctids replace the crangonyctids in extreme eastern Asia, where the latter are almost entirely absent (see Holsinger 1986b:fig. 1). The present range of *Pseudocrangonyx,* which encompasses parts of the northeastern Asian mainland and the Japanese Islands, probably reflects an earlier, continuous distribution of this genus in freshwater habitats throughout the region. Separation of the Japanese Islands as slivers from the Asian continent by tectonic activity beginning in the middle Tertiary (see Dott & Batten 1976) would have isolated populations in Japan from those on the mainland. Based on the assumption that *Pseudocrangonyx* is an old subterranean freshwater inhabitant, it is highly unlikely that any of these insular populations were established by recent invasions from marine waters.

Acknowledgments

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NEW GENERA IN THE THALASSINIDEAN FAMILIES CALOCARIDIDAE AND AXIIDAE (CRUSTACEA: DECAPODA)

Brian Kensley

Abstract.—The family Calocarididae Ortmann, 1891, is resurrected and rediagnosed. Three characters distinguish members of the family: hermaphroditism, eye reduction, and second pleopods having enlarged appendices masculinae along with loss of the distal endopod. The first pleopods are spatulate and somewhat plow-shaped, a character also seen in some axiids. Four genera are included in the Calocarididae: *Calastacus, Calocaris, Callistocaris,* and *Lophaxius,* the latter two being described as new. Two new genera in the Axiidae are described: *Posthonocaris* and *Sakaiocaris.* A scheme for the derivation of the Calocarididae from more generalized axiids such as the two newly-described genera, is proposed.

The families and many of the genera of the Thalassinidea are extremely poorly defined, with little sense of phylogeny in the currently accepted classification. The Axiidae in particular contains several more or less well diagnosed and probably polyphyletic genera. In the course of a phylogenetic study of the thalassinideans, it became clear that a group of four genera of axiids were more closely related to each other than to the rest of the family. Almost 100 years ago, Ortmann (1891), placed one of these genera in a separate family, the Calocaridae, but this taxon received no recognition and has not been used in the last 50 years. This family is now resurrected and rediagnosed for this group of four probably monophyletic genera.

Calocarididae Ortmann, 1891

Calocaridae Ortmann, 1891:47, 50.—Stephensen, 1910:75, 77, 189.—Runnström, 1925:14.

Type genus.—*Calocaris* Bell, 1853.

Diagnosis.—Hermaphroditic, generally deepwater forms, with eyes showing some reduction and loss of both pigment and ommatidial facets. Linea thalassinica absent. Maxilla 2 scaphognathite bearing spinulose whip. Maxilliped 3 bearing dentate ischial crest. Pereopods lacking exopods. Pereopods 1 and 2 chelate. Pleopodal rami elongate-slender. Pleopod 1 always present, of 2 articles, directed anteromesially along posterior thoracic sternites, with distal article broadened and flattened, and bearing proximomesial cluster of hooks (fused appendix interna). Pleopod 2 present, showing loss of distal endopod, enlargement of appendix masculina, and eventual fusion of appendix interna with appendix masculina. Uropodal outer ramus with transverse suture.

Genera.—*Calastacus* Faxon, 1893; *Callistocaris,* new genus; *Calocaris* Bell, 1853; *Lophaxius,* new genus.

Remarks.—Ortmann (1891) designated the new family Calocaridae, characterized by four features: rostrum flat, triangular; pleopodal rami narrow; outer uropodal ramus with suture; podobranchs and mastigobranchs present on pereopods. Ortmann further suggested that eventually two subfamilies, the Calocarinae and the Laomidiinae, would need to be distinguished. Stephensen (1910), in a rather obscure semi-popular handbook, used the name Calocaridae as a family of the Anomura, though not designating an author. His diagnosis, loosely translated, reads: "The large chelae have straight long fingers, but no tubercles. Two pairs of legs have chelae. Suture across outer branches of uropod. (*Footnote—By a misfortune this suture was dropped from fig. 51). Only one genus and species with us" [presumably meaning 'in Denmark']. Following this diagnosis, is a short discussion and figure of *Calocaris macandreae* Bell. The only other use of the name Calocaridae I have been able to trace, is that of Runnström (1925). This family name (in corrected form), is now resurrected, and its diagnosis expanded, to include several related genera, but not the genera of the Laomidiidae, which are markedly different.

Calastacus Faxon, 1893

Calastacus Faxon, 1893:194.—Borradaile, 1903:539.—de Man, 1925:8, 116.—Balss, 1957:1580.—de Saint Laurent, 1972:353, 354.

Type species.—By monotypy, *Calastacus stilirostris* Faxon, 1893:194.

Diagnosis.—Hermaphroditic. Carapace: supraocular spine present; post-cervical carina and spines lacking; rostrum at lower level than anterior carapace; rostral margins unarmed (except for supraocular spine); median carina entire; submedian carina lacking; lateral carina present only as short posterior extension of lateral rostral margins. Eye lacking pigment, stalk equal to or shorter than cornea. Antennal acicle a slender, elongate spike.

Maxillipeds: exopods on 1–3; epipods on 1–3, with small podobranch on 3; 2 arthrobranchs on 3.

Pereopods: lacking exopods; epipods on 1–4, small podobranchs on 1–3; 2 arthrobranchs on 1–4; pleurobranchs lacking; propodi and dactyli of 3–5 cylindrical, not expanded; pereopod 1 chelipeds slightly asymmetrical, not sexually dimorphic; pereopod 2 chelate; pereopods 3–5, dactyli simple.

Pleopods: rami elongate-slender; appendix interna present on 2–5; pleopod 1 of 2 articles, distal article broad, plow-shaped, appendix interna represented by small mesial lobe bearing hooks; pleopod 2 with small appendix interna fused with basal article of appendix masculina; both articles of latter with double row of setae on mesial margin.

Uropod: outer ramus with transverse dentate suture.

Telson: lacking dorsal spines, longer than wide.

Species.—

Calastacus laevis de Saint Laurent, 1972. Bay of Biscay, north-east Atlantic, 950–1000 m.

Calastacus stilirostris Faxon, 1893. Pacific Mexico, 1208 m.

Callistocaris, new genus

Type species.—By present designation, *Calocaris alcocki* (McArdle, 1900).

Etymology.—The generic name is derived from the Greek "kallistos"—most beautiful, plus "karis"—a shrimp. Gender: feminine.

Diagnosis.—Hermaphroditic. Carapace: strong supraocular spine present; postcervical carina and spines lacking; rostrum set slightly lower than anterior carapace; rostral margins armed; median carina entire; submedian carina entire; lateral carina entire posterior to supraocular spine. Eye lacking pigment, anteriorly flattened, with mesiodistal tubercle; eye and stalk not differentiated. Antennal acicle fairly well developed, spike-like, but considerably less than half length of peduncle article 4.

Maxillipeds: exopods and epipods (no podobranchs) on 1–3; 2 arthrobranchs on 3.

Pereopods: exopods lacking; epipods on 1–4, podobranchs lacking; 2 arthrobranchs on 1–4; pleurobranchs lacking; propodi and dactyli of 3–5 not expanded; pereopod 1 chelae symmetrical, lacking gape between fingers; pereopod 2 chelate; dactyli of 3–5 simple. Branchiae simple, lacking pinnae.

Pleopods: rami elongate-slender, appendix interna lacking on 3–5, pleopod 1 uniramous, biarticulate, distal article bilobed, with small mesial patch of hooks; pleopod 2 appendix masculina with indication of fusion of 2 articles, with double row of spines along mesial margin, and with appendix interna fused basally.

Uropod: outer ramus with transverse nondentate suture.

Telson: longer than wide, lacking dorsal spines.

Species.—

Callistocaris aberrans (Bouvier, 1905). Off St. Lucia, Lesser Antilles, 809 m.

Callistocaris alcocki (McArdle, 1900). Bay of Bengal, 992 m.

Callistocaris cf. *alcocki* (McArdle, 1900). SW Indian Ocean, 1000 m.

Calocaris Bell, 1853

Calocaris Bell, 1853:231.—Ortmann, 1891: 50, pl. 1, fig. 5d–i.—Borradaile, 1903: 539.—de Man, 1925:7, 114.—Balss, 1957: 1580.—de Saint Laurent, 1972:353, 354.

Type species.—By monotypy, *Calocaris macandreae* Bell, 1853:233.

Diagnosis.—Hermaphroditic. Carapace: supraocular spine part of lateral rostral spine series; post-cervical carina entire; rostrum at slightly lower level than anterior carapace; rostral margins armed; median carina entire; submedian carina absent; lateral carina armed. Eye lacking pigment, stalk and cornea not differentiated; anteriorly flattened and contiguous along midline. Antennal acicle reduced to barely visible scale.

Maxillipeds: exopods and epipods on 1–3; reduced podobranch on 2 and 3; 2 arthrobranchs on 3.

Pereopods: lacking exopods; epipods on 1–4, small podobranchs on 1–3; 2 arthrobranchs on 1–4; pleurobranchs lacking; propodi and dactyli of 3–5 not expanded; pereopod 1, chelae subsimilar, symmetrical, not sexually dimorphic, broad gape between fingers; pereopod 2 chelate; pereopods 3–5 dactyli simple.

Pleopods: pleopod 1 of 2 articles, distal article expanded, lobed, with patch of hooks on small mesiodistal lobe; pleopod 2, endopod lacking distal portion, appendix masculina slender, mesially setose, of single article, appendix interna articulating at its base.

Uropod: outer ramus with transverse nondentate suture.

Telson: longer than wide, with or lacking two rows of submedian non-articulating dorsal spines.

Species.—

Calocaris barnardi Stebbing, 1914. Off Saldanha Bay, South Africa, 89–180 m. Off Namibia, 338 m.

Calocaris granulosus Grebenyuk, 1975. Gulf of Alaska.

Calocaris macandreae Bell, 1853. Mediterranean; North-east Atlantic, 25–1072 m.

Calocaris sp. Indian 'form' of *C. macandreae* (see Alcock, 1901): Bay of Bengal, Arabian Sea.

Calocaris templemani Squires, 1965. Northwest Atlantic, Newfoundland, Gulf of Maine, 260 m.

Lophaxius, new genus

Type species.—By present designation, *Lophaxius rathbunae,* new species (=*Calastacus investigatoris* Rathbun, 1904, *non* Anderson, 1896).

Etymology.—The generic name is derived from the Greek 'lophos,' a crest or mane, referring to the post-cervical mid-dorsal ridge of the carapace, plus the frequently-used 'axius.' Gender: masculine.

Diagnosis.—Hermaphroditic. Carapace: supraocular spine (part of lateral rostral series) present; post-cervical carina with irregular tubercles present; rostrum at slightly lower level than anterior carapace; rostral margins armed; median carina entire; submedian carina absent; lateral carina only extending short distance posterior to rostrum, with one or two spines. Cornea unpigmented, not flattened; stalk subequal to cornea in length. Antennal acicle short. Maxillipeds 1–3 with exopods and epipods; large podobranch on 2 and 3; 2 arthrobranchs on 3.

Pereopods: exopods lacking; epipods on 1–4, with large podobranch on 1–3; 2 arthrobranchs on 1–4; pleurobranchs lacking; pereopod 1 symmetrical, fingers of chelae gaping basally; pereopod 2 subchelate; dactyli of 3–5 simple.

Pleopods: rami elongate-slender; appendix interna present on 2–5; pleopod 1 of 2 articles, distal article spatulate, with small mesial patch of hooks; pleopod 2, appendix masculina slender, tapering, setose, with appendix interna articulating at its base.

Uropod: outer ramus with transverse non-dentate suture.

Telson: longer than wide, with dorsal non-articulating spines.

Species.—

Lophaxius investigatoris (Anderson, 1896). Arabian Sea, 1733 m.

Lophaxius rathbunae, new species. North-eastern Pacific, Alaska to California, 549–1190 m.

Remarks.—*Lophaxius* resembles *Calastacus* in having non-pigmented eyes, and with the cornea not flattened as in *Calocaris*. It differs from typical *Calastacus* in having spines on the rostrum, pleopod 1 not as broadly plow-shaped, the appendix masculina of pleopod 2 not as modified, the appendix interna free, in having a well developed postcervical carina, and in having the chela of pereopod 1 with a gap between fingers as in *Calocaris.*

Lophaxius rathbunae, new species

Calastacus investigatoris Rathbun, 1904: 151, *non* Anderson, 1896.—Schmitt, 1921:112, fig. 75, *non* Anderson, 1896.

Diagnosis.—Carapace, palm of first chela, abdominal somites, uropods, and telson tuberculate. Merus of pereopod 1 with about 10 spines on anterior (upper) margin, eight spines on posterior (lower) margin. Outer uropodal ramus with six spines on outer margin; inner uropodal ramus with two or three spines on outer margin.

Material.—Syntypes, USNM 28316, cl 19.5 mm, *Albatross* sta 3347, off Cascade Head, Oregon, 631 m.—USNM 28317, cl 19.1 mm, *Albatross* sta 3210, south of Dannakh Islands, Alaska, 884 m.—USNM 28318, ovig. cl 18.4 mm, 17.1 mm, *Albatross* sta 2928, off San Diego, California, 763 m.—USNM 155734, cl 17.1 mm, *Albatross* sta 4352, off San Diego, California, 979–1005 m.

Remarks.—The species *Calastacus investigatoris* Anderson, 1896, from 1733 m in the Arabian Sea is, from the description and figure (Alcock & Anderson 1896:pl. 25, fig. 1) remarkably similar to the north-eastern Pacific species, but differs in having weaker spination on the anterior and posterior margins of the merus of the first chelipeds, and in lacking marginal teeth on the inner uropodal ramus. No doubt further differences would be apparent, were material of the Indian Ocean species available. Indeed, Rathbun (1904:151) mentioned that not all the eastern Pacific specimens agreed with Alcock's description; she also noted some variability in the specimens at her disposal. Given the vast distance between the Indian and Pacific Ocean records, and the differences noted, the two species cannot be regarded as conspecific.

Key to genera of the Calocarididae

1. Post-cervical carina or ridge present on carapace 2
– Carapace lacking post-cervical carina 3
2. Eyes flattened, mesially contiguous .... *Calocaris*
– Eyes rounded, not mesially contiguous .... *Lophaxius*
3. Eyes rounded; appendix masculina mesially setose .... *Calastacus*
– Eyes flattened; appendix masculina mesially spinose .... *Callistocaris*

Axiidae Huxley, 1878
Posthonocaris, new genus

Type species.—By present designation, *Axius rudis* Rathbun, 1906.

Etymology.—The generic name is a combination of the Greek 'posthon'—one having a large penis (referring to the large appendix masculina), plus 'karis'—a shrimp. Gender: feminine.

Diagnosis.—Gonochoristic, but with hermaphroditic forms occurring in the population. Carapace: cervical groove present; postcervical carina and spines absent; rostral margins armed; median carina entire; submedian carina dentate; lateral carina entire (apart from supraocular spine). Eyes well pigmented; eyestalk rounded, longer than or subequal to cornea. Antennal acicle a well developed spike.

Maxillipeds: exopods on 1–3; epipod present on 1 and 2; 3 with epipod plus podobranch, two arthrobranchs.

Pereopods: exopods absent; pereopods 1–3 with epipod plus podobranch; pereopod 4 with epipod only; two arthrobranchs on 1–4; one pleurobranch on 2–4. Pereopod 1 chelae asymmetrical. Pereopods 3–5, dactyli simple.

Pleopods: Rami elongate-slender. Pleopod 1 in female slender-elongate, of 2 articles, distal article bearing marginal setae; pleopod 1 of male or hermaphrodite spatulate, of 2 articles, distal article bearing proximomesial clump of hooks; pleopod 2 of male or hermaphrodite with distal setose portion of endopod somewhat reduced, appendix masculina and appendix interna articulating at about midlength of endopod, appendix masculina elongate, setose, reaching well beyond apices of endopod and exopod; pleopods 3–5 lacking appendices internae.

Uropod: Outer ramus with transverse dentate suture.

Telson: With non-articulating dorsal spines; single posterolateral articulating spine.

Species.—

Lophaxius longipes (Bouvier, 1905), off Barbados, 225 m.

Lophaxius rudis (Rathbun, 1906), off Hawaii, 73–426 m.

Sakaiocaris, new genus

Type species.—By present designation, *Axiopsis brucei* Sakai, 1986.

Etymology.—The generic name is a combination of 'sakai,' for Dr. Katsushi Sakai, plus the Greek 'karis'—a shrimp. Gender: feminine.

Diagnosis.—Males, females, and hermaphroditic forms occurring in same species. Carapace: cervical groove present; post-cervical carina a low rounded ridge lacking spines or tubercles; rostral margins dentate; median carina dentate; submedian carina dentate; lateral carina dentate. Eye with reduced pigmentation; eyestalk rounded. Antennal acicle a well developed spike.

Maxillipeds: 1–3 with epipod and exopod, 2–3 with reduced podobranch; two arthrobranchs on 3.

Pereopods: exopods lacking; epipod plus podobranch on 1–3; epipod only on 4; two arthrobranchs on 1–4; one pleurobranch on 2–4. Pereopod 1, chelae asymmetrical. Pereopod 2 chelate. Pereopods 3–5, dactyli simple.

Pleopods: Pleopod 1 of male of 2 articles, distal article spatulate, with proximomesial clump of small hooks. Pleopod 1 in female (and in only hermaphrodites seen), slender, elongate, of 2 articles, distal article bearing marginal setae; pleopod 2 in male with large exopod and endopod, setose appendix masculina and appendix interna both articulating proximally on endopod. Pleopods 3–5 with free appendix interna.

Uropod: outer ramus with dentate transverse suture.

Telson: with non-articulating dorsal spines; with two articulating postero-lateral spines.

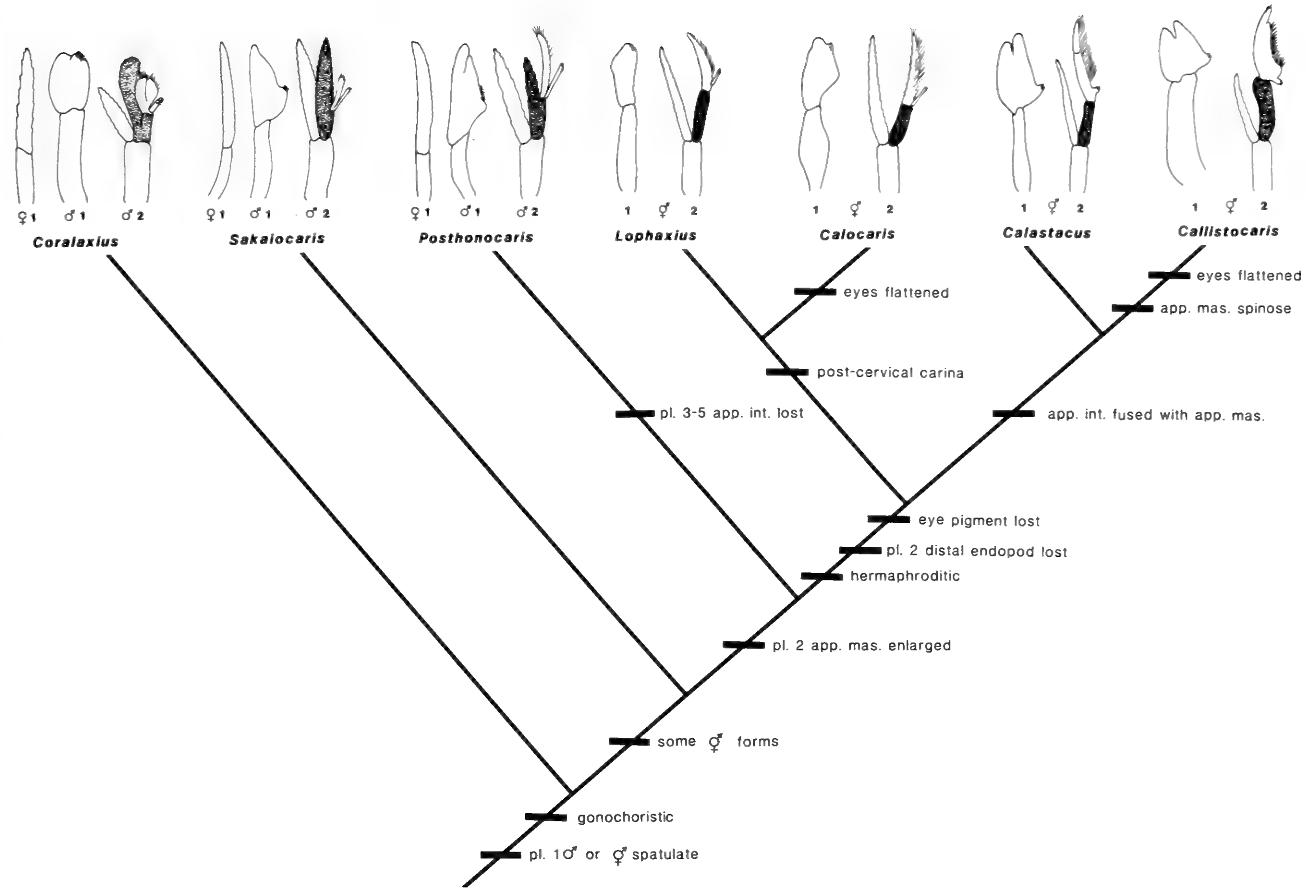

Fig. 1. Hypothetical scheme for derivation of the Calocarididae from more generalized Axiidae, illustrating pleopods 1 and 2, and changes in character-states. Endopod of pleopod 2 shaded. (Abbreviations: app. int.—appendix interna; app. mas.—appendix masculina; pl.—pleopod.)

Species.—

Sakaiocaris brucei (Sakai, 1986); off Western Australia, in hexactinellid sponges, 296–458 m.

Discussion

Three synapomorphies separate the Calocarididae from the Axiidae (s.l.). 1. Invariable hermaphroditism. 2. Enlargement of the appendix masculina of pleopod 2, along with loss of the setose distal element of the endopod. 3. Eye reduction and loss of eye pigment.

A possible pathway in the development of hermaphroditism, from purely gonochoristic forms (e.g., *Coralaxius*), through forms having some hermaphrodites in the population (e.g., *Posthonocaris, Sakaiocaris*), to purely hermaphroditic forms (*Calocaris, Calastacus, Callistocaris, Lophaxius*), is illustrated in Fig. 1. *Coralaxius* Kensley & Gore, 1981, is purely gonochoristic, and possesses sexually dimorphic first pleopods. In the male, the first pleopod is uniramous and biarticulate, the distal article being spatulate and having a clump of mesial hooks. These latter are presumed to come from the appendix interna which has fused with the endopod; the exopod has either been lost or has fused with the endopod. It is postulated that the genera *Posthonocaris* and *Sakaiocaris* have hermaphroditic forms in the population. In these, the first pleopod of the female or protandrous hermaphrodite is a slender setose, uniramous, biarticulate structure, while in the males, a spatulate first pleopod very similar to those found in the Calocarididae is seen. The presence of protandrous hermaphrodites in populations of decapod species has been well documented. Policansky (1982) mentions a variety of decapod crustaceans in which protandry occurs, including *Calocaris macandreae* in which the biology, and especially reproduction, has been well examined (see Wollebaek 1909, Runnstrom 1925, Buchanan 1963). Bauer (1986) reported the presence of primary males, primary females, and protandric hermaphrodites that pass through a male phase, a transitional phase, and then become breeding females, in the hippolytid caridean shrimp *Thor manningi.* While ten specimens of *Sakaiocaris brucei* and four specimens of the two species of *Posthonocaris* form too small a sample on which to state with certainty that protandrous hermaphrodites occur in these populations, the dimensions of the specimens (at least of the former species) would seem to suggest this. The only ovigerous female of *S. brucei* seen has a carapace length of 21.9 mm; the three hermaphrodites with their female first pleopods measure 16.1, 19.6, and 20.0 mm (suggesting that these are either in the transitional phase or approaching the breeding female phase), while five males range from 13.8–23.3 mm.

Posthonocaris seems to represent a more advanced stage than *Sakaiocaris,* in this supposed trend towards hermaphroditism. This is seen in the reduction of the setose distal portion of endopod of pleopod 2, an elongation of the proximal non-setose portion, and marked enlargement of the appendix masculina. In the fully hermaphroditic calocaridids *Calastacus* and *Callistocaris,* the final stage of this trend, with complete loss of the distal endopod, and enlargement and specialization of the appendix masculina, with which the appendix interna has fused, can be seen.

There would seem to be a correlation between development of hermaphroditism and depth distribution in this group of thalassinideans. *Coralaxius,* with its spatulate first pleopod in the male, is a shallow (11–76 m) coral reef inhabitant. *Sakaiocaris* inhabits hexactinellid sponges in 296–456 m. Perhaps there is a reproductive advantage in having a hermaphroditic phase in this species, given its cryptic habit. Species of *Posthonocaris* have been recorded in depths of 73–426 m; *Calocaris* from 89–1072 m; *Callistocaris* from 809–1000 m; *Calastacus* from 970–1208 m; *Lophaxius* from 1733 m.

Loss of eye pigment and corneal facets, along with a breakdown of the distinction between cornea and stalk, can be seen in the four genera of the Calocarididae, suggesting loss of function linked to increased depth distribution. The hypothetical scheme proposed in Fig. 1 requires that anteriorly flattened eyes arose independently in *Calocaris* and *Callistocaris,* which is not unfeasible. Similar flattening of eyes can be seen in several decapod groups such as cave-dwelling hippolytid shrimps, deepsea bresiliid shrimp, as well as in the stomatopod genus *Bathysquilla* (R. B. Manning, pers. comm.).

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THREE NEW SPECIES OF COLOMBIAN LACE BUGS OF THE GENERA *LEPTODICTYA* AND *LEPTOPHARSA* (HETEROPTERA: TINGIDAE)

Richard C. Froeschner

Abstract.—Three new species of lace bugs from Colombia are described and illustrated by habitus drawings: *Leptodictya fuscipes* collected on an unidentified species of Poaceae; *Leptopharsa madrigali* found on *Phaseolus* species (Fabaceae); and *Leptopharsa reflexa* taken on *Roupala "glabriflora"* (Proteaceae).

A small collection of lace bugs representing samplings of environments in the vicinity of crop fields in Colombia was submitted by Dr. Raul Velez-Angel, Universidad Nacional, Medellin, Colombia, for identification. In it were three species new to science. Neither of the two genera involved here has had a recent key to aid in identification of the numerous species included in the Drake & Ruhoff (1965) catalog: *Leptodictya* Stal with 52 species and *Leptopharsa* Stal with 105 species. Construction of such keys at this time is impractical, but as names are needed for making known more information about these insects, they are described here.

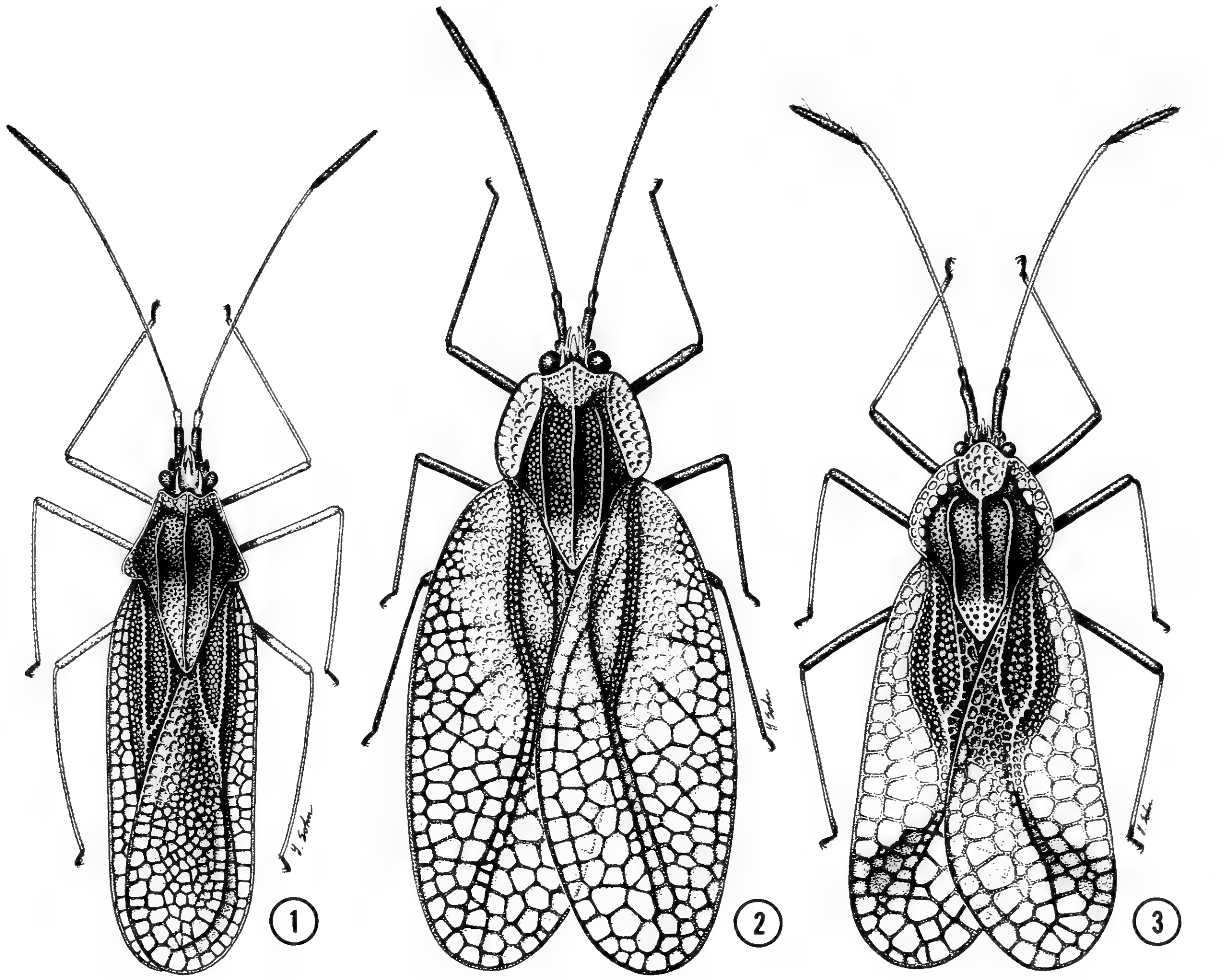
Leptodictya fuscipes, new species
Fig. 2

Diagnosis.—This species belongs among those forms of *Leptodictya* in which the costal area has embrowned veins everywhere except in a broad band adjacent to and along the full length of the discoidal area; veins in this area are milky white and together form a sort of halo around the discoidal areas. *L. fuscipes* can be distinguished most readily from all other members of the group by the strongly embrowned limiting veins of the discoidal area plus the nearly black femora.

Description.—Length 4.5–5.1 mm. Head, surface of pronotum except apical half of posterior projection, and under surface of body black, these parts usually coated with a dense white pruinosity. Antenna blackened except for the slightly paler apex of segment III. Bucculae, except narrow margins, black. Legs deep brown to black. Paranota and anteromedian cyst mostly milky white, outermost vein (along fold) of paranotum and mediodorsal vein of cyst light brown. Longitudinal pronotal carinae light brown. Hemelytral cells hyaline; veins delimiting discoidal area, of costal area (except for the broad band along discoidal area), and of most of sutural area fuscous to black; discoidal area with a faintly but distinctly embrowned diagonal line across midlength. Sternal laminae yellow.

Head deflexed, with 5 elongate pale spines directed forward or slightly obliquely upward: occipital pair; pair above base of clypeus; and one spine on midline of dorsum of head. Antennal segment I about as long as head, twice as long as II; III 4.5 times as long as I + II; IV slightly less than half as long as III. Labium attaining posterior end of mesosternal laminae.

Pronotum with anteromedian cyst tectate, as high as median carina, anteriorly produced medially as a right angle attaining medlength of eyes, posteriorly extending almost to apex of interhumeral convexity. Lateral longitudinal carinae very low, with a single row of punctiform cells; median carina twice as high as lateral carinae, uniseriate.



Figs. 1–3. 1, *Leptopharsa reflexa* new species, actual length 3.5 mm. 2, *Leptodictya fuscipes* new species, actual length 4.5 mm. 3, *Leptopharsa madrigali* new species, actual length 3.8 mm.

Discoidal area confined to basal half of hemelytron, with 4–5 cells across greatest width. Costal area with 4 usually prominent, regular, nearly straight cross veins between which are numerous irregular cells; cells in milky area along discoidal area distinctly reduced. Hypocostal laminae uniseriate.

Peritreme obliquely transversely auriculate, reaching hypocostal lamina. Sternal laminae absent from prosternum, present and subparallel on mesosternum, present and forming a cordate outline on metasternum. Abdomen convex, impunctate.

Holotype male, Colombia; "Cocorna (Ant. [ioquia]), Agt. 1981, A. Madrigal, en Graminea," deposited in the National Museum of Natural History. Paratypes (deposited in Universidad Nacional, Medellin, Colombia, and National Museum of Natural History): 1 male, 2 females with same data as holotype.

The species name directs attention to the dark fuscous to black legs.

Leptopharsa madrigali, new species
Fig. 3

Diagnosis.—Among those species of *Leptopharsa* with divergent hemelytra (apices, at rest, not completely overlapping, see Fig. 3) this species may be recognized by the combination of 2 regular rows of subequal cells in the costa along the basal three-fourths of the discoidal area; the short occipital spines which do not surpass the antennal insertions; and the wholly blackened femora.

Description.—Length 3.4–4.0 mm. Head, pronotal surface (except pale posterior apex), and body ventrally black. Antennal segments I and IV black, II brown, III yellow. Bucculae black except for yellow ventral row of cells. Femora, extreme ends of tibiae, and tarsi black; most of tibia yellow. Pronotal outgrowths (paranota, longitudinal carinae, and anteromedian cyst) mostly yellow with hyaline cells. Discoidal and subcostal areas with most veins black. Costal area, including veins, pale except for fuscous band radiating posterolaterally from darkened base of membranal area. Sternal laminae yellow.

Head vertically deflexed, with 5 forward directed short spines: occipital spines decumbent, not or just reaching antennal insertions; a pair of supraclypeal spines, a single spine above bases of latter pair. Antennal segment I about as long as width of head across eyes; II almost a third as long as I and twice as long as wide; III about 4 times as long as I + II; IV about two-thirds as long as III. Labium reaching posterior ends of mesosternal laminae.

Pronotum with anteromedian cyst inflated, slightly higher than median carina, extending almost to apex of head, extending less than half way up anterior slope of interhumeral convexity. Longitudinal carinae very low, composed of a single row of puncturelike cells. Paranotum biseriate, outline convex around humerus, thence straight or weakly convex almost to rounded anteroapical angle.

Hemelytron with costal margin weakly convexly diverging on basal fifth, thence straight and diverging to apical fourth. Discoidal area confined to basal two-fifths of hemelytron, with 5 cells across greatest width. Subcostal area with 4–5 cells across greatest width. Costal area biseriate along basal three-fourths of discoidal area, irregularly 3–4 cells wide beyond apex of discoidal area. Hypocostal lamina uniseriate.

Peritreme obliquely transversely auriculate, reaching hypocostal lamina. Sternal laminae present on all 3 sterna, low uniseriate, more widely separated on meta- than on pro- or mesosterna; sternal groove not interrupted by transverse carina. Abdomen convex, impunctate.

Holotype, male, Colombia; "Urrao (Ant. [ioquia]), Mar. 1977, A. Madrigal C., en *Phaseolus* sp." (Fabaceae), deposited in the United States National Museum of Natural History. Paratypes deposited in the Universidad Nacional, Medellin, Colombia, and the National Museum of Natural History; 2 females with same data as holotype; 3 females, La Estrella (Ant. [ioquia]) Colombia, April 1985, A. Madrigal on Fabaceae; 1 male and 1 female, Coldos (Ant. [ioquia]), Colombia, Nov. 1973, A. Madrigal, on Fabaceae.

The species name dedicates this lace bug to the Colombian entomologist, A. Madrigal C., who obtained this type series and has done much to increase knowledge of Heteroptera in Colombia.

Leptopharsa reflexa, new species

Fig. 1

Diagnosis.—Among the species of *Leptopharsa* in which the sutural areas overlap at rest (apices not divergent, see Fig. 1), this new species belongs to a group characterized by the following features: 1) 3–5 long cephalic spines; 2) low, tectate (in no way swollen) anteromedian cyst separated from the higher median longitudinal pronotal carina by a deep angulation; 3) a narrow (1–2 rows of cells) paranotum continued at same width around humerus and then incurved and abruptly terminated to form a distinct angle with the posterior pronotal projection; and 4) a biseriate costal area.

The 7 species in the group diagnosed with the above enumeration of characters can be separated by the following couplets:

1. Pronotum with prominent, projecting anterolateral angles, its anterior margin as wide or wider than head across eyes 2

– Pronotum without distinct anterolateral angles, its anterior margin narrower than width of head across eyes 6

2. Height of longitudinal pronotal carinae over crest of inter-humeral convexity greater than diameter of femur . . . . *tenuis* (Champion)

– Height of longitudinal pronotal carinae over crest of interhumeral convexity less than diameter of a femur 3

3. Occipital spines decurved, decumbent, cylindrical, apices blunt, not surpassing antennal insertions . . . . *albella* Drake

– Occipital spines long, tapering to acute apices, projecting obliquely away from head and extended beyond antennal insertions 4

4. Head with 5 spines: a pair of short spines immediately below the median supraclypeal spine plus a pair of occipital spines 5

– Head with 3 spines: a median supraclypeal spine and a pair of occipital spines . . . . *avia* Drake

5. Antennal segment I short, about twice as long as length of eye. Dorsal aspect darker: head, pronotal surface, and generally veins of discoidal area lightly but distinctly embrowned . . . . *fica* Drake

– Antennal segment I long, about 2 and a half times as long as length of eye. Dorsal aspect whitish to faintly yellowed (a few veins sometimes darkened) . . . . *delicata* Monte

6. Paranotum vertically reflexed, free margin straight from anterior end of prominent humerus . . . . *reflexa,* new species

– Paranotum weakly obliquely elevated, free margin convex from humerus to anterior end . . *elegantula* Stal

Description.—Length 3.3–3.6 mm. Head, pronotal surface (except anterior margin and most of posterior projection) black, these surfaces may be covered with a light coating of white pruinosity. Antennal segments I and IV black, II and III reddish yellow. Buccule mostly white. Legs, except black tarsi, reddish yellow. Pronotum with anteromedian cyst, longitudinal carinae, and paranota yellow, cells hyaline to lightly enfumed. Hemelytral veins mostly yellow, those in discoidal and subcostal areas sometimes brown. Sternal laminae pale yellow.

Head vertically deflexed, with 5 cephalic spines: pair of decurved, decumbent occipitals reaching antennal insertions; supraclypeal pair and median spine directed anteriorly. Antennal segment I slightly shorter than length of head, twice as long as II, III nearly 5 times as long as I + II, IV one third as long as III. Labium reaching posterior ends of mesosternal laminae.

Pronotum with anteromedian cyst small, lower than median longitudinal carina, forming a short angulation above base of head, posteriorly terminated between calli, not ascending interhumeral convexity. Longitudinal carinae low, uniseriate, median one slightly higher posteriorly. Paranotum vertically reflexed, wholly biseriate or in part uniseriate; free margin straight from anterior end to projecting humerus.

Hemelytra with apices overlapping, axes and costal margins parallel. Discoidal area 4–5 cells wide, confined to basal two-fifths of hemelytron. Subcostal area 3–4 cells wide. Costal area biseriate along basal three-fourths, uniseriate on apical fourth. Hypocostal lamina uniseriate.

Peritreme small, weak, transversely auriculate, reaching hypocostal lamina. Laminae present on all 3 sterna, straight and parallel on pro- and mesosterna, more widely separated and bowed convexly outward on metasternum; sternal groove not interrupted by transverse carina. Abdomen convex, impunctate.

Holotype male, Colombia, "Guarne (Ant.[ioquia]), Jun 1978, A. Madrigal C., en *Roupala glabriflora*" (Proteaceae), deposited in the United States National Museum of Natural History. Paratypes: 4 males, same data as holotype, deposited in Universidad Nacional, Medellin, Colombia, and in National Museum of Natural History.

The species name was suggested by the vertically reflexed paranota.

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KROHNITTELLIDAE AND BATHYBELIDAE, NEW FAMILIES IN THE PHYLUM CHAETOGNATHA; THE REJECTION OF THE FAMILY TOKIOKAISPADELLIDAE AND THE GENERA *TOKIOKAISPADELLA, ZAHONYA,* AND *ABERROSPADELLA*

Robert Bieri

Abstract.—New monogeneric families are proposed for the genera *Krohnittella* and *Bathybelos* (Krohnittellidae and Bathybelidae). The family Tokiokaispadellidae is considered invalid because the type species is a misidentified *Pterosagitta draco.* Morphologic changes in poorly preserved chaetognaths are described, and the genera *Zahonya* and *Aberrospadella,* based on poorly preserved specimens, are considered invalid.

After compiling a comprehensive list of approximately 100 species in 22 genera currently included in the phylum Chaetognatha, it became clear to me that the genus *Kronittella* has not been assigned to any extant family and the genus *Bathybelos* is so exceptional that it cannot be included in any extant family. Therefore, to correct these inconsistencies I propose the following two new families.

Krohnittellidae, new family

Diagnosis.—The family lacks both anterior and posterior teeth. A single pair of lateral fins, completely rayed, partly on the trunk and partly on the tail do not reach the ventral ganglion. No ventral transverse musculature.

Discussion.—The family is monogeneric containing the single genus, *Krohnittella* Germain & Joubin, 1912. The authors based their new genus on two specimens taken in a 4000 m net tow that possibly struck bottom in the eastern North Atlantic. Because more than 60 years passed before the genus was reported again, considerable doubt existed about its validity. Tokioka in his 1965 revision retained it as valid, but did not assign it to any known family. Bieri (1974) rediscovered the genus in the eastern North Pacific where a single, nearly mature specimen in good condition was caught with an opening-closing sled trawl at 2000 m in the San Clemente Basin. The lack of ventral transverse musculature and teeth clearly differentiate the family from the Eukrohniidae and Spadellidae. Salvini-Plawen (1986), unaware of Bieri's (1974) paper, suggested that the genus may belong to *Bathyspadella.* The lack of transverse musculature in *Krohnitella* is irreconcilable with *Bathyspadella* which in any case is the junior genus. Although the names are similar, there is no confusion with the family Krohnittidae whose members have a single pair of flabelliform teeth among other distinguishing characteristics.

Bathybelidae, new family

Diagnosis.—No ventral ganglion but rather a dorsal ganglion. Two pairs of lateral fins completely lack fin rays. One paired row of teeth which are highly curved. Eyes vestigial.

Discussion.—The family is monogeneric containing the single genus, *Bathybelos.* In her paper describing the genus, Owre (1973) (=Michel) referred to the dorsal nerve ganglion as a cerebral ganglion but in her later description (Michel 1984) she referred to it as a rectangular nerve center. I think dorsal ganglion or nerve center is more accurate than cerebral because it is posterior to the apparent location of the vestigial eyes and is more in the position of the corona ciliata. In all known chaetognaths the cerebral ganglion is well anterior to the eyes (Goto & Yoshida 1987). The second unique feature of this species is the complete lack of rays in the lateral fins. All other known chaetognaths, except the problematic *Aberrospadella* discussed below, have some rays in the lateral fins. These characters and the presence of only one paired row of teeth differentiate it from the families Sagittidae, Eukrohniidae, and Spadellidae.

Status of the Family Tokiokaispadellidae

In 1986 Salvini-Plawen erected a new family, Tokiokaispadellidae to contain *Tokiokaispadella lata* Kassatkina, 1980. The original type genus of the family is incorrectly given as *Tokiospadella,* apparently a typographical error (Salvini-Plawen 1986: 126). It is clear that the single specimen which formed the basis of Kassatkina's new genus and species is nothing more than a poorly preserved specimen of the common species *Pterosagitta draco,* ubiquitous in the tropical and semitropical oceanic waters of the world.

In Kassatkina's (1980) description of the new species, taken in a 0–14 m net tow in a lagoon north of New Guinea, the posterior fin reaches only to the transverse septum and is completely rayed as in *P. draco.* There are two paired rows of teeth as in *P. draco.* The tooth and hook formula agrees with that given by Alvariño (1967) for *P. draco.* The collarette is narrow and extends from the neck to the tail fin. In perfectly preserved specimens of *P. draco,* the collarette extends onto the tail fin and is nearly as broad on each side as the body width. But as E. L. Michael (1919) pointed out long ago, the collarette is usually eroded to varying degrees. Sometimes it is completely missing. It is very rare to find *P. draco* with a completely intact collarette and almost never are the "wings" of the collarette preserved (Bieri 1966). In Kassatkina's specimen the collarette is partly stripped away, the usual situation when relatively coarse meshed nets are used or the net is towed faster than about 25 cm per second.

The ovaries are short and immature and there is no indication of seminal vesicles. Her figure shows large gut diverticulae but Alvariño (1967) stated that in *P. draco* the diverticulae are small and incipient. Kassatkina's drawing shows the corona ciliata extending well up onto the head between the eyes, but in the text states that it is entirely on the trunk. Aida (1897) and Grassi (1883) show the corona entirely on the trunk whereas Ghirardelli (1952) showed it extending onto the head. Tokioka (1940) showed the corona in three figures. In two of the figures it is on the trunk, but in the largest figure it is partly on the head.

Thus there are no characters which differentiate this species from *P. draco* except the ventral transverse musculature, the very short tail segment, and the relatively great body width. None of these characters were listed in Salvini-Plawen's extremely short diagnosis of the new family.

Tokioka (1952:312) in discussing the transverse musculature of the enigmatic genus *Zahonya,* wrote, "It is a noteworthy fact that some species with strongly developed musculature assume an appearance, when they are in a slightly contracted state, as if they were provided with a transverse musculature along the whole body." Nagasawa & Nemoto (1985) discussed the distortion of chaetognaths probably due to attack by bacteria. They documented the shortening of the body length by 50% but did not describe the appearance of pseudo-transverse musculature. My own experience convinces me that if chaetognaths are trawled for more than half an hour, some specimens will be seriously damaged and distorted not just by physical abrasion but also by bacterial attack as discussed by Nagasawa and Nemoto, and by biochemical lysis after death. If the plankton sample is not preserved immediately upon retrieval from the sea, distorted individuals may compose from a few to all of the plankton sample. Chaetognaths that die before preservation and are left unpreserved for more than a few minutes develop contracted longitudinal muscles that have a series of interuptions that look superficially like transverse muscles as Tokioka reported. I have seen this condition in almost every species of chaetognath from samples throughout the Pacific and from the Arctic Ocean. The specimens lose their characteristic crystalline transparency and become chalky-white in reflected light or opaque-grey in transmitted light. The body loses its tubular shape and becomes flattened dorsoventrally, sometimes to an extreme degree. The body is often distorted into an arc. The tail segment often shortens extremely and becomes relatively wider before the trunk deteriorates. The shortening of the body length can be extreme, specimens of *Flaccisagitta hexaptera* that would normally be 40 mm long can shorten to 20 mm. The head may become greatly shortened and thus appear relatively wider, with the jaws thrown widely apart, and the neck constricted.

Thus the three characters which might possibly distinguish Kassatkina's *Tokiokaispadella* from *Pterosagitta draco,* transverse musculature, short tail segment, and relatively wide body, in my opinion, are artifacts. The genus *Tokiokaispadella* and the family Tokiokaispadellidae based upon it are both invalid.

Status of the Genera *Zahonya* Oye, 1918 and *Aberrospadella* Kassatkina, 1971

In 1918 van Oye described a new species and genus from the Java Sea, *Zahonya cestoda.* No one has found an example of this species since the original description; however, it has been mentioned in review articles, for example, Tokioka (1965). It seems remarkable that almost no one (Tokioka 1952 excepted) has recognized this species for what it is, a poorly preserved individual showing all the characteristics of the genus *Sagitta* (sensu Ritter-Záhony, 1911) except for the transverse musculature which clearly is an artifact of morbidity before killing with a preservative. Oye's description and drawing are not adequate to distinguish the specimen from the more than 25 epiplanktonic species of sagittids that occur in that region, although Tokioka's supposition (1952) that it might be a small individual of *Sagitta robusta* or *Sagitta ferox* is a reasonable one. Thus, *Zahonya cestoda* is best left as a nomen dubium with the genus *Zahonya* a junior synonym of *Sagitta.*

In 1971 Kassatkina described a new genus and species, *Aberrospadella verruculosa* from Possjet Bay in the Sea of Japan near Vladivostok. The description is based on two contorted specimens 1.4 mm and 3.4 mm long. No seminal vesicles nor ovaries are present. The specimens almost certainly are poorly preserved or diseased individuals of *Parasagitta elegans.* Only the rayless lateral fins, rayless tail fin and the supposed transverse musculature differentiate the species from juvenile *Parasagitta elegans* (see Kotori 1975 for detailed descriptions of early larval stages of *Parasagitta elegans*). The species has two sets of teeth and the number of hooks agrees with *P. elegans* at that size. As Kotori showed, *P. elegans* emerges from the egg with one pair of lateral fins. In juvenile *P. elegans* the collarette is massive, the ventral ganglion is relatively very large, and the tail segment relatively large, all characteristics of *Aberrospadella verruculosa.* Gut diverticulae are present in both species. Although the absence of rays in the fins is something of an enigma, until the species is redescribed based on mature specimens that are clearly in an excellent state of preservation, this species is a nomen dubium and the genus a junior synonym of *Parasagitta.*

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HANSENOTHURIA BENTI, NEW GENUS, NEW SPECIES (ECHINODERMATA: HOLOTHUROIDEA) FROM THE TROPICAL WESTERN ATLANTIC: A BATHYAL, EPIBENTHIC HOLOTHURIAN WITH SWIMMING ABILITIES

John E. Miller and David L. Pawson

Abstract.—*Hansenothuria benti,* new genus, new species, is described and illustrated from material collected with the Research Submersibles *Johnson-Sea-Link* I and II on bathyal slopes of the Bahama Islands at depths of 639–904 m. This species was also observed at St. Vincent, Lesser Antilles, at depths of 363–447 m. On several occasions, *H. benti* has been observed to swim in response to physical disturbance.

From 1983 to 1988, in collaboration with Dr. Gordon Hendler (Los Angeles County Museum—LACM) and Porter M. Kier (Director Emeritus, National Museum of Natural History, Smithsonian Institution—SI), we studied the composition and ecology of the echinoderm fauna of the bathyal slopes of the Bahama Islands using the research submersibles *Johnson-Sea-Link* (JSL) I and II (Harbor Branch Oceanographic Institution, Inc.—HBOI). A total of 84 dives was made to depths of 200–904 m, and the diverse echinoderm fauna, comprising at least 180 conspicuous species, was sampled, photographed, and videotaped. Of the 10 bathyal holothurian species encountered, one of the most common proved to be a new genus and species of the Family Synallactidae. In April 1989, after this paper was accepted for publication, the authors participated in a JSL expedition to the Lesser Antilles, and this new species was again observed, on seven of 10 dives conducted off the west coast of St. Vincent. It is of particular interest for it has the ability to swim when disturbed. It is a facultative swimming species (sensu Miller & Pawson 1990) whose swimming behavior is described in detail elsewhere (Miller & Pawson 1990).

The Family Synallactidae has a worldwide distribution in bathyal and abyssal depths, and at present it comprises approximately 15 genera and 120 species. Synallactid genera and species are usually difficult to characterize, and the family is in urgent need of a thorough revision. Under these circumstances we are reluctant to erect a new genus for the species described here, but its unique diagnostic features preclude referral of the species to any of the existing confamilial genera.

Methods

The JSL submersibles carry four passengers to a maximum depth of 904 m for 3–5 h per dive. Each submersible is equipped with an array of sophisticated tools that allow the occupants to sample, photograph, and videotape benthic or pelagic organisms. During a dive, several environmental parameters, for example temperature, conductivity and depth, are automatically monitored and recorded at intervals preselected by the scientist. Additional information on the submersibles can be found in Askew (1984).

For in situ photography, we used a laser-aiming device (Fig. 2, U.S. Patent #4,


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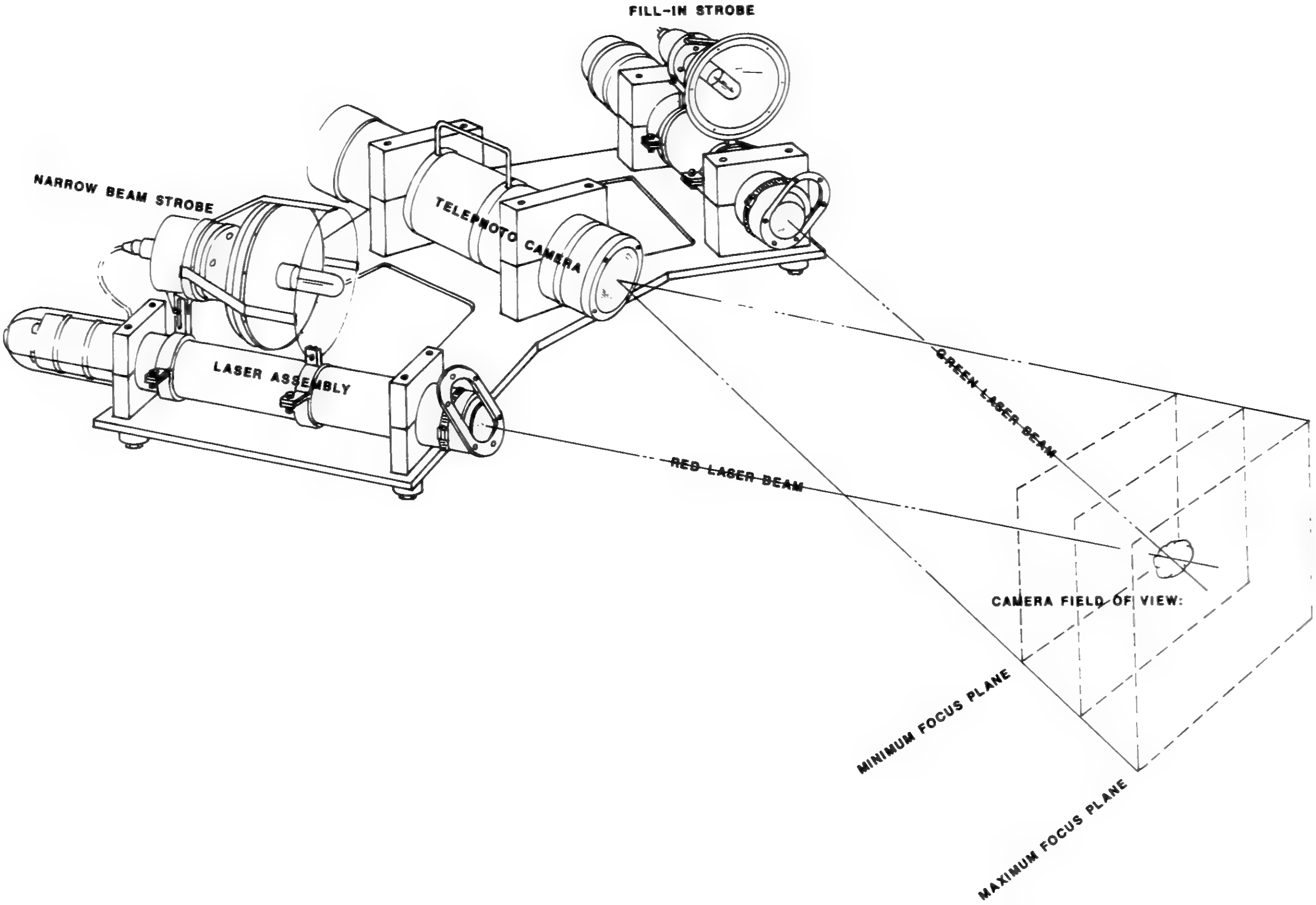

Fig. 2. Diagram of laser-aimed camera system (U.S. Patent #4,777,501) developed for the *Johnson-Sea-Link* submersibles to photograph benthic organisms at bathyal depths.

777,501) developed by HBOI engineers to aim and focus a Benthos camera system (Model 372) on the animals being studied. A detailed description of the laser-aiming system is found in Caimi & Tusting (1987). Because the distance between the film plane and the subject photographed remained constant throughout a dive, we were able to calculate the exact field of view in each photograph and thereby determine the precise length of living specimens prior to collection.

Order Aspidochirotida Grube, 1840

Family Synallactidae Ludwig, 1894

Hansenothuria, new genus

Diagnosis.—Body fragile, translucent, semi-cylindrical, tapering gently anteriorly and posteriorly, four to five times as long as broad. Ventral surface flat, body arched, middorsal interradial area depressed. Ventrolateral margin fringed with short to long papillae joined by continuous brim; brim broadest anteriorly, where component po-

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Fig. 1. *Hansenothuria benti,* new genus and species: *In situ* photographs—A, French Bay, San Salvador Is., JSL-I-2005, 694 m, TL = 20.3 cm; B, off Plana Cays, JSL-I-2274, 829 m, TL = 17.2 cm; C–E, swimming postures, off Cockburn Town, San Salvador Is., JSL-I-2331, 649 m, TL = 23.0 cm, bright streak to left of posterior end of specimen in E is sediment-laden mucus strand shed by active swimming movements; F, Fernandez Bay, San Salvador Is., JSL-I-2048, 759 m, TL = 16.5 cm; G, Fernandez Bay, San Salvador Is., JSL-I-2048, 759 m, TL = 21.5 cm. Photo credit for C–G: C. Young and L. Cameron, HBOI.

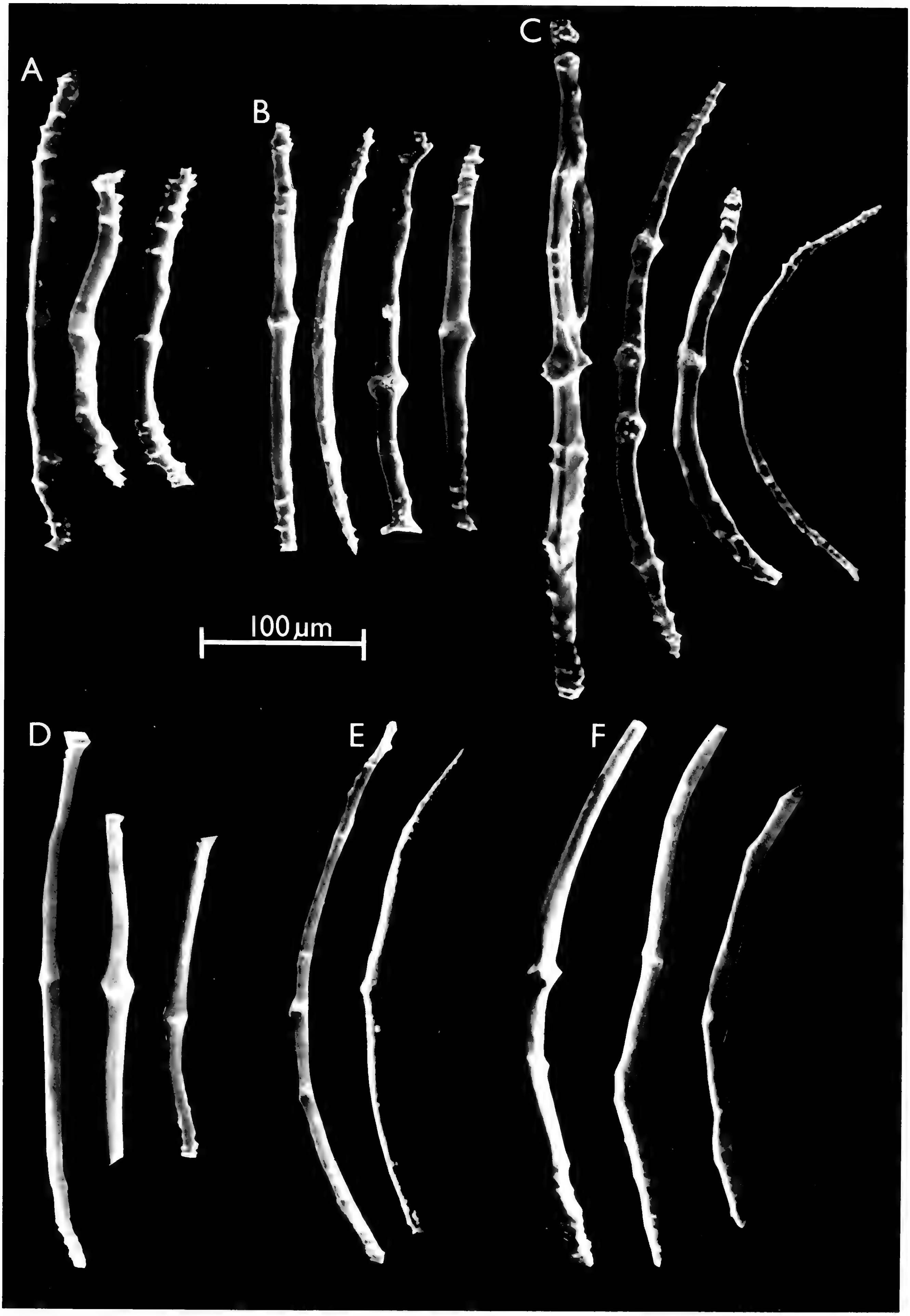
Table 1.—Material examined/observed and distribution data for *Hansenothuria benti,* new genus, new species.

Dive No.	Date	Locality[1]	Coordinates	Depth (m)	No. individuals collected/observed	Total length (cm)	Submersible observers
JSL-II-808	09-IV-84	S of Cross Harbor Pt., Great Abaco Island	25°52.20′N 77°15.5′W	700 699	2	10.8 (PR) 12.5 (PR)[2]	J. Miller M. Flake
JSL-II-813	12-IV-84	N of Egg Island	25°30.85′N 76°55.10′W	739	1	NR	D. Pawson T. Askew
JSL-I-1647	13-VIII-85	NW of Crooked Island	22°47.75′N 74°23.50′W	791	6+	NR	K. Reinhart D. Liberatore
JSL-II-1699	07-XI-85	Fernandez Bay, San Salvador Island	24°03.30′N 74°33.05′W	659	1	12.8 (PO)	L. Cameron M. Flake
JSL-I-1705	10-XI-85	Off Cockburn Town, San Salvador Island	24°04.35′N 74°33.30′W	762 691 711 707	4	10.1 (PO) 13.9 (PO) 14.9 (PO) ≈20 (PO)	L. Cameron D. Liberatore
JSL-I-1904	25-X-86	W of Black Rock	26°14.84′N 77°42.35′W	677	1	NR	L. Cameron C. Caddigan
JSL-I-1960	15-III-87	Off Nassau Harbor, New Providence Island	25°06.47′N 77°20.67′N	657	1	11.2 (PR)	S. Pomponi M. Adams
JSL-I-2005	23-IV-87	French Bay, San Salvador Island	23°55.05′N 74°31.67′W	694	1	20.3 (PO)	D. Pawson M. Adams
JSL-I-2009	25-IV-87	Off Cockburn Town, San Salvador Island	24°03.20′N 74°33.33′W	694	1	10.0 (PO)	J. Miller C. Caddigan
JSL-I-2048	16-V-87	Fernandez Bay, San Salvador Island	24°03.30′N 74°33.10′W	759	2	16.5 (PO) 21.5 (PO)	L. Cameron M. Adams
JSL-II-1497	18-X-87	Off Morgan's Bluff, Andros Island	25°12.20′N 77°59.93′W	639	1	NR	G. Hendler T. Askew
JSL-II-1503	22-X-87	Off Nassau Harbor, New Providence Island	25°06.43′N 77°23.81′W	666 744	2	18.0 (PO) 18.4 (PO)	L. Cameron M. Adams
JSL-II-1515	27-X-87	N of Egg Island	25°30.85′N 76°55.10′W	691	many	1 measured 18.4 (PO)	C. Young M. Adams
JSL-I-2264	13-IX-88	Off Riding Rock, San Salvador Island	24°03.61′N 74°33.37′W	903 904 895	3	8.0 (PR) 12.0 (PR) 15.0 (PR)	D. Billett D. Liberatore

Table 1.—Continued.

Dive No.	Date	Locality[1]	Coordinates	Depth (m)	No. individuals collected/observed	Total length (cm)	Submersible observers
JSL-I-2274	18-IX-88	W of Plana Cays	22°36.5′N	829	5	17.2 (PO)	G. Hendler
			73°38.6′W	821		20.3 (PO)	C. Caddigan
				817		21.5 (PO)	
				814		2 (NR)	
JSL-I-2331	21-X-88	Off Cockburn Town, San Salvador Island	24°02.50′N	649	1	23.0 (PO)	L. Cameron
			74°32.35′W				D. Liberatore
JSL-I-2332	21-X-88	Off Cockburn Town, San Salvador Island	24°02.50′N	644	1	NR	J. Piraino
			74°32.35′W				D. Liberatore
JSL-I-2340	25-X-88	N of Egg Island	25°27.52′N	610	1	NR	B. Bingham
			76°54.32′W				D. Liberatore

1—all localities in the Bahama Islands; St. Vincent data not included here.
2—selected as holotype; TL of live specimen = ≈20 cm.
NR—not recorded.
PO—TL determined from seafloor photograph.
PR—TL determined from preserved material.


A
B
C
100 µm
D
E
F

dia may reach 25 mm length. Midventral radius naked; ventrolateral radii with numerous, minuscule hair-like feet in two or three rows. Each lateral dorsal radius with 10–31 short (15 mm), sharply pointed papillae arranged in slightly zigzag row. Excepting endplates in ventral feet, ossicles exclusively simple rods, occurring only in tentacles, papillae and feet. Gonad as two tufts of tubules, one to each side of dorsal mesentery.

Remarks.—*Hansenothuria* superficially resembles some species of the genera *Bathyplotes* Östergren, 1898 and *Paelopatides* Théel, 1886 in body shape and in possessing a marginal brim that aids in swimming but it differs from these genera, and most other synallactid genera, in possessing very simple body wall ossicles. *Hansenothuria* further differs from *Bathyplotes* in having a dorsally positioned anus, and from *Paelopatides* in lacking feet along the midventral radius. Ossicles appear to be consistently absent from *Benthothuria* Perrier, 1898 and *Paroriza* Herouard, 1923; neither of these genera seems to bear any close relationship to *Hansenothuria.*

Type species.—*Hansenothuria benti,* new species, designated herein.

Etymology.—The genus name is of feminine gender. This holothurian is named for our friend and colleague, the late Dr. Bent Hansen, Zoological Museum, Denmark, in recognition of his superb contributions to our knowledge of deep-sea holothurians.

Hansenothuria benti, new species

Figs. 1, 3; Tables 1, 2

Diagnosis.—As for the genus. Color in life variable, light blue to pale purple; dorsal papillae translucent to black.

Material examined.—Collection and locality data for the Bahama Islands specimens/photographs studied during our dives aboard *Johnson-Sea-Link* I and II are presented in Table 1. Due to the delicate nature of this species, it was difficult to preserve; accordingly only a few specimens collected preserved well enough to be catalogued as museum material. The following specimens have been deposited at the National Museum of Natural History, Smithsonian Institution (USNM), the Indian River Coastal Zone Museum, HBOI (IRCZM) or the Los Angeles County Museum of Natural History (LACM).

Holotype: USNM E38201, 12.5 cm total length (TL), JSL-II-808, 699 m.

Paratypes: one specimen, USNM E38202, 10.8 cm TL, JSL-II-808, 700 m; one specimen, USNM E38203, 10.0 cm TL, JSL-I-2009, 694 m; one specimen, USMN E38204, 8.0 cm TL, JSL-I-2264, 903 m; one specimen, IRCZM 71:00447, 12.0 cm TL, JSL-I-2264, 904 m; two specimens, USNM E38205, too damaged to measure, JSL-I-2274, 814 m; one specimen, USNM E38206, 20.3 cm TL, JSL-I-2274, 821 m; USNM E38207, 21.5 cm TL, JSL-I-2274, 817 m; one specimen, LACM 88-205.1, 15.0 cm TL, JSL-I-2264, 895 m.

External morphology.—Subcylindrical species of moderate size; 13–23 cm TL in life, approximately four to five times as long as broad (Fig. 1D). Body fragile; body wall thick, gelatinous, transparent; internal structures (intestine, Fig. 1A, G; gonad, Fig. 1C–E) usually visible through body wall. Anterior and posterior ends gently tapering; anterior end high, bluntly rounded (Fig. 1B), posterior end low, narrowed to form short "tail" (Fig. 1A). Ventral surface a flattened sole with minute, hairlike tube feet along

←

Fig. 3. Scanning electron micrographs of skeletal ossicles from *Hansenothuria benti:* A–C (holotype of 12.5 cm TL, measured preserved) A, Rods from dorsal papillae; B, Rods from ventrolateral papillae; C, Rods from tentacles; D–F (paratype of 10 cm TL, measured from seafloor photograph) D, Rods from dorsal papillae; E, Rods from ventrolateral papillae; F, Rods from tentacles.

Table 2.—Length of skeletal rods in appendages of *Hansenothuria benti.* n, number of ossicles measured; $\bar{x}$, mean; SD, standard deviation; ossicles taken from holotype, 12.5 cm TL (preserved length).

Length (μm) of rods from:	n	$\bar{x}$	SD	Range
Lateral papillae of brim	25	155.6	34.4	109.3 – 230.2
Dorsal papillae	25	180.5	41.1	109.3 – 260.5
Ventrolateral feet	25	226.6	59.3	114.0 – 376.7
Tentacles	25	266.6	67.6	178.8 – 423.5

lateral radii (Fig. 1C–E); midventral radius naked. Ventrolateral margin composed of brim of webbed podia (Fig. 1F). Brim widest at anterior and posterior ends of body (Fig. 1D). Bodywall high with steep-sloping sides; dorsal interradius distinctly sunken, forming shallow trough between radii (Fig. 1A). Each dorsal radius with 10–31 slender, hair-like papillae with pointed tips (Fig. 1A, B, E–G). Papillae regularly spaced in slightly zigzag rows, extending along length of body. Number of papillae per radius tending to increase with size of specimen. Papillae completely contractile, varying in length up to 15 mm. Mouth ventral, at extreme anterior end (Fig. 1C–E), surrounded by 20 peltate tentacles. Tentacles, short, with thick trunks, terminating in flat, circular disks. Anus dorsal, situated just above posterior brim (Fig. 1C).

Internal anatomy.—Holotype (USNM E38201) and one paratype (USNM E38202) dissected to examine internal features; both specimens lacking intestinal tract and respiratory trees. *Holotype* (male): Two bulbous polian vesicles attached to circum-oral water ring. Gonad in 2 tufts, one on each side of dorsal mesentery; each tuft with upwards of 10 tubules, some branching 2-3 times, others unbranched. Tubules extending posteriorly for two-thirds length of body cavity. Radial longitudinal muscles unequally developed; dorsal muscles larger than ventral.

Paratype (female): Gonad apparently fully developed, tubules up to 30 mm TL. Tubules swollen throughout length, filled with eggs in germinal vesicle stage. Eggs dense, yolky, subspherical; measuring up to 600 μm in diameter. Longitudinal muscle bands divided; those to either side of dorsal mesentery with four bundles of strands; remaining three bands with two bundles each.

Ossicles (see Table 2 for measurements).—Only two ossicle types occur in body wall. Simple rods present in dorsal papillae (Fig. 3A, D), papillae of lateral brim (Fig. 3B, E), tentacles (Fig. 3C, F), and ventral feet. Rods straight to curved, with one or more enlarged areas near middle, and few to several spinules near ends. Average length of rods from tentacles and ventral feet considerably longer than those from dorsal and lateral papillae (Table 2). Delicate end plate ossicles, composed of two or more pieces, in tube feet; plates have polygonal perforations and irregular, scalloped margins.

Coloration.—Bodywall coloration varying from light blue to pale purple; smaller specimens generally lighter colored than larger individuals. Marginal brim of webbed papillae appears transparent (Fig. 1F), usually lacking pigment. Black flecks scattered on dorsal surface, especially along mid-dorsal interradius and on dorsal papillae. Fully extended dorsal papillae grey; contracted papillae appear black. Ventrally, bodywall transparent to white with scattered black flecks along each lateral radius and on some tube feet (Fig. 1C, D). Tentacles white; gonadal tubules, visible through body wall posterior to mouth on ventral surface (Fig. 2C–E), also white.

Habitat.—All specimens collected or observed at the Bahamas (see Table 1) occurred in the upper bathyal zone (639–904 m) on slopes ranging from ca. 5° – 60°. Sediment composition at collecting sites varied from a thin layer of biogenic sand covering a limestone pavement to a thick layer of silty sand with scattered coral and algal (*Halimeda* spp.) rubble. Off the west coast of St. Vincent, *H. benti* was encountered at depths of 363–447 m, on fairly steep slopes (ca. 30°–50°) covered with terrigenous silty sand.

Distribution.—*Hansenothuria benti* is at present known from the Bahama Islands at depths of 639–904 m, and from St. Vincent in the Lesser Antilles at depths of 363–447 m. Our submersible observations were restricted to depths of less than 904 m; it is likely that the species occurs at greater depths and on bathyal slopes of other Caribbean islands.

Behavior.—Swimming specimens of *Hansenothuria benti* were observed and videotaped on several occasions. Swimming activity was at first observed after three specimens were captured by the submersible and placed in collection bins for the ascent to the surface. While in the bin, the holothurians swam by flexing and curling the anterior and posterior ends of their bodies. This behavior continued for at least two hours. On several subsequent dives, swimming *H. benti* were videotaped; this species is a facultative swimmer (sensu Miller & Pawson 1990) which spends the majority of its time on the seafloor, venturing upwards into the water column only in response to physical disturbance, e.g., prodding. No individuals of *H. benti* were swimming when first encountered. Swimming behavior in this species is most likely an adaptation to avoidance of predators or physical hazards, such as sediment slumping. A detailed account of active swimming movements in *H. benti* is provided in Miller & Pawson (1990).

Remarks.—Of the 10 holothurian species encountered during our dives in the Bahamas, only the pelagothuriid elasipod *Enypniastes eximia* Théel was found to occur in greater abundance than *Hansenothuria benti* at the depths studied. C. Young and L. Cameron (HBOI, pers. comm.) report seeing as many as six or seven individuals within an area of approximately 225 m^2 (the estimated area visible to the occupants of the JSL's forward compartment when visibility is 15 m). At St. Vincent, *H. benti* is a common component of the megabenthos; it was the most frequently observed holothurian on our dives, with densities reaching a peak of four to six individuals/10 m^2.

Because *H. benti* is a relatively large and common component of the epibenthic invertebrate fauna, it might seem surprising that no individuals of this species were taken by earlier workers sampling the seafloor with dredges and trawls. The explanation for this may lie in the fact that even specimens collected with care by the submersible and carried to the surface in seawater-filled containers arrive aboard ship in very poor condition. During the journey from the seafloor to the surface, the holothurian's epidermal and dermal tissues begin to slough off, and frequently the entire external bodywall is completely autotomized, leaving internal organs surrounded by the longitudinal and circular muscle layers.

Acknowledgments

The authors wish to express their gratitude to their colleagues in the Bahamas echinoderm project, Drs. Gordon Hendler and Porter M. Kier for their assistance. We thank the crews of the *Johnson-Sea-Link* submersibles and the Research Vessels *Johnson, Seward Johnson,* and *Edwin Link* for their dedicated cooperation during several research missions to the Bahama Islands and the Lesser Antilles. We are grateful to C. Young and L. Cameron and to researchers of the Division of Marine Biotechnology at HBOI for supplying us with specimens, photographs, videotapes, and locality data of *Hansenothuria benti* from their submersible programs. Funding for submersible dives was granted through the following organizations (principal investigators listed in parentheses): HBOI (J. Miller, C. Young, S. Pomponi); National Science Foundation (C. Young, L. Cameron); Smithsonian Institution (J. Miller, D. Pawson). The following HBOI employees are gratefully acknowledged for their patience and perseverence in developing the laser-aimed camera system used in this research: F. Caimi, C. Chulamanis, T. Couture, C. Tietze, R. Tusting. T. Smoyer, HBOI, was most helpful in producing the color plate (Fig. 1). Figure 2 was rendered by J. Hastings, HBOI. P. Linley, HBOI, assisted with photography of the ossicles (Fig. 3). This paper is HBOI Contribution No. 714 and Smithsonian Institution Marine Station at Link Port Contribution No. 247. Contribution No. 14—Studies on bathyal echinoderms of the Bahama Islands, J. E. Miller (HBOI), Principal Investigator.

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ETHEOSTOMA (NOTHONOTUS) WAPITI (OSTEICHTHYES: PERCIDAE), A NEW DARTER FROM THE SOUTHERN BEND OF THE TENNESSEE RIVER SYSTEM IN ALABAMA AND TENNESSEE

David A. Etnier and James D. Williams

Abstract.—A new percid fish, *Etheostoma wapiti,* a member of the *E. maculatum* species group, is described from two tributaries to the Tennessee River in northwest Alabama and south central Tennessee. This rare darter, known from 55 specimens, is most closely related to *E. vulneratum* from which it differs in details of pigmentation and squamation. *Etheostoma vulneratum,* formerly treated as a subspecies of *E. maculatum* or *E. sanguifluum,* is elevated to species level based on phylogenetic analysis of the *maculatum* species group and subgenus *Nothonotus.* Comments on the former distribution and the remaining habitat of *E. wapiti* are presented.

In our (Williams & Etnier 1978) description of *Etheostoma aquali* we briefly considered the identity of three juvenile *Nothonotus,* one specimen collected in 1963 from Elk River at Fayetteville, Lincoln County, Tennessee, and two specimens collected in 1884 from Shoal Creek, Florence, Lauderdale County, Alabama. We suspected at that time that these specimens represented an undescribed species of the *E. maculatum* species group. No additional specimens were taken in a survey of the Elk River fishes by Jandebeur (1972) or in the several additional collections from the Elk River and Shoal Creek systems prior to 1980. Our hopes of eventually locating an extant population and seeing adults were renewed when Charles F. Saylor provided a juvenile from a Tennessee Valley Authority collection from Elk River Mile 41, Giles County, Tennessee, and another from Elk River Mile 40.8. A University of Tennessee Regional Faunas Class located a population in lower Richland Creek, a major Elk River tributary, in May 1981 where an adult female and a juvenile were collected. We revisited the Richland Creek locality in June 1982, in anticipation of finally capturing an adult male in or near breeding condition. We were most interested in whether the red pigment patterns of adult males would be drastically different from those of other members of the *E. maculatum* species group. We were able to collect five adult males which to our great surprise completely lacked the bright red body spots and red fin markings typical of other members of the species group. Subsequent to discovery of the Richland Creek population, main channel Elk River populations have been located at one site in Lincoln County and two sites in Giles County, Tennessee, associated with anthropogenic limestone rubble, and at one site in Lincoln County, Tennessee and two sites in Limestone County, Alabama, where natural limestone bedrock formations abut or cross the river. At present there are only 55 known specimens of this rare but distinctive darter.

Phylogenetic analysis of subgenus *Nothonotus,* particularly the *Etheostoma maculatum* species group, indicates that both *E. sanguifluum* (Cope) and *E. vulneratum* (Cope) should be treated as species rather than as subspecies.

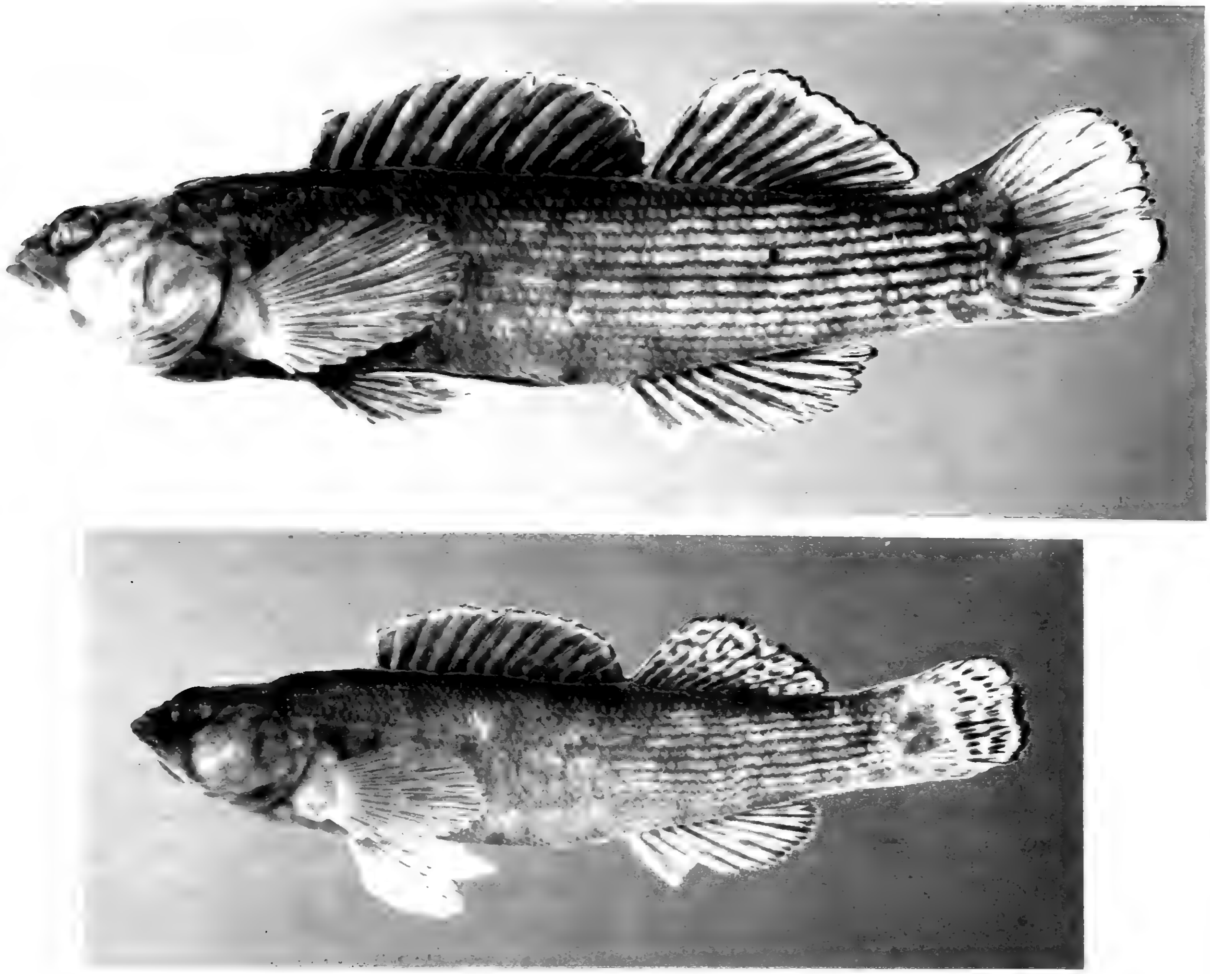

Fig. 1. *Etheostoma wapiti,* new species, holotype, USNM 288069, male, 71 mm SL (upper specimen) and allotype, USNM 288070, female, 55 mm SL (lower specimen).

Type material of *Etheostoma wapiti* is deposited in the collections of the American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), Cornell University (CU), Illinois Natural History Survey (INHS), University of Kansas (KU), Tulane University (TU), University of Alabama (UAIC), Florida State Museum (UF), University of Michigan (UMMZ), National Museum of Natural History, Smithsonian Institution (USNM), and the University of Tennessee (UT). Comparative material of other species of *Nothonotus* from the collections at USNM and UT were utilized in the preparation of this description. Methods described by Hubbs & Lagler (1958) were used in obtaining counts and measurements except diagonal scale counts were made according to the techniques of Raney & Suttkus (1964). Vertebral counts were made using the methods of Bailey & Gosline (1955). Swofford's (1984) PAUP program, version 2.3, was used for phylogenetic analysis. Outgroups utilized include genus *Percina* and *Etheostoma* subgenera *Allohistium* and *Litocara* for polarizing characters within genus *Etheostoma,* with subgenus *Oligocephalus,* the hypothesized sister group of *Nothonotus,* used as outgroup for assessing polarity of additional characters within *Nothonotus.* As our primary objective was to assess relationships within the *E. maculatum* species group (*aquali, maculatum, microlepidum, moorei, rubrum, sanguifluum, vulneratum, wapiti*), we treated each outgroup as a single taxon, utilizing the most

Table 1.—Standard length (mm), and proportional measurements (in thousandths of SL) of the holotype (male) and four other males and five females of *Etheostoma wapiti,* new species. $\bar{x}$ = mean.

	USNM 288069 holotype	Males		Females	
		$\bar{x}$	Range	$\bar{x}$	Range
Standard length	70.8	62.6	57.2–70.8	52.2	46.0–57.7
Body depth at dorsal-fin origin	215	218	213–223	232	217–251
Caudal peduncle depth	138	138	133–145	129	126–135
Caudal peduncle length	220	220	213–228	217	213–222
Pelvic fin length	168	179	168–189	191	185–200
Pectoral fin length	201	205	199–215	220	212–231
Head length	266	266	253–278	272	262–276
Snout length	71	70	67–74	72	68–75
Orbit length	66	67	66–69	72	69–74
Upper jaw length	71	76	71–83	74	73–76
Longest dorsal-fin spine	130	127	120–134	126	120–132
Longest dorsal-fin ray	145	151	145–156	146	142–150
1st anal-fin spine	95	98	95–105	101	97–105
Longest anal-fin ray	144	151	144–156	150	137–167

widespread character state as typical for the taxon. For instance, in *Oligocephalus* only *E. radiosum* has dark margins on median fins and only *E. pottsi* and *E. swaini* have caudal peduncle depth approximating that of *Nothonotus.* In these cases, the character coded for *Oligocephalus* was, respectively, median fins lacking dark margins, and caudal peduncle slender (see Phylogenetic Analysis, characters 2, 8).

Etheostoma wapiti, new species
Boulder Darter
Fig. 1, Tables 1–3

Etheostoma rufilineatum Gilbert, 1891:151. Two of five specimens from Shoal Creek, Florence, Alabama.

Etheostoma microlepidum Raney & Zorach, 1967:93. Specimens from Shoal Creek, Florence, Alabama.

Etheostoma (*Nothonotus*) sp. Starnes & Etnier, 1986. Endemic in Tennessee River drainage.—Biggins, 1987, 1988. Endangered status proposed and finalized, respectively, under U.S. Endangered Species Act.

Holotype.—Adult male, USNM 288069, 70.8 mm standard length (SL), Richland Creek at County Road 4209 crossing, 11.2 air miles south-southeast of Pulaski, Giles Co., Tennessee, 7 Jun 1982, W. C. Dickinson, D. A. Etnier, M. A. Etnier, C. E. Louton, J. A. Louton, W. C. Pennington.

Allotype.—Adult female, USNM 288070, 55 mm SL, taken with holotype.

Paratopotypes.—Paratypes taken with primary type are TU 148010 (2), UMMZ 213950 (2), and UT 91.3469 (1). Additional paratypes taken at the type locality are UT 91.2203 (2), 22 May 1981.

Other paratypes.—Elk River system, Tennessee: TU 30271 (1), 11 Apr 1963, and UT 91.3459 (1), 13 Sep 1988, Elk River Mile 89.7, Fayetteville, Lincoln Co., 0.25 miles below U.S. Highway 231 bridge. AMNH 58257 (2), ANSP 162645 (2), CAS 64178 (2), CU 71707 (2), and KU 22122 (5), Elk River Mile 61.0, Hamilton Mill, Lincoln Co., 13 Sep 1988. INHS 68229 (3), 14 Apr 1985, and UT 91.3075 (1), 25 Jun 1986, mouth of Indian Creek at Elk River Mile 52.5, Giles Co. UT 91.80 (1), Elk River Mile 41.0, Giles Co., 7 Oct 1980. UT 91.2628 (1), Elk River Mile 40.8, Giles Co., 2 Aug 1983. UT 91.3072 (4) and UF 44921 (4), Elk River Mile 52.5, at mouth of Indian Creek, Giles Co., 25 Jun 1986. UT 91.3084

Table 2.—Frequency distribution, sample size, and means of selected scale counts in *Etheostoma wapiti, E. aquali, E. vulneratum,* and Elk River system *E. camurum.* Counts for *E. aquali* from Williams & Etnier (1978) and *E. vulneratum* from Zorach & Raney (1967).

	Lateral line scales																					
	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	n	$\bar{x}$
E. wapiti						1	3	1	2	5	7	3	7	7	12	—	2	—	1	1	52	61.65
E. aquali								1	1	3	7	17	6	6	4	6	3	3			57	62.21
E. vulneratum		1	2	3	2	7	9	14	9	9	7	5	3	—	2	1	2				76	57.87
E. camurum	2	—	—	3	2	5	2	5	2	1	1	1	1								25	55.88

	Anal-fin origin to first dorsal fin									
	13	14	15	16	17	18	19	20	n	$\bar{x}$
E. wapiti			1	1	8	18	18	7	53	18.36
E. aquali				5	13	23	13	3	57	17.93
E. vulneratum	1	3	14	23	16	10	6	3	76	16.57
E. camurum			3	13	5	3			24	16.33

	Second dorsal-fin origin to anal fin								
	13	14	15	16	17	18	19	n	$\bar{x}$
E. wapiti		4	9	23	7	8	1	52	16.17
E. aquali	1	16	26	13	1			57	14.95
E. vulneratum	8	11	30	23	4			74	15.19
E. camurum		8	7	8	1			24	15.08

	Caudal peduncle scales									
	18	19	20	21	22	23	24	25	n	$\bar{x}$
E. wapiti				6	14	20	10	3	53	22.81
E. aquali				2	28	13	10	3	56	22.71
E. vulneratum		3	6	15	26	18	8		76	21.97
E. camurum	2	9	3	8	2				24	19.96

(7), Elk River Mile 36.7, Giles Co., 17 Oct 1986.

Elk River system, Limestone Co., Alabama: UAIC 7851.01 (4), Elk River Mile 30.7, about 3 miles above Smith Hollow Road (Alabama highway 127) bridge, 24 Oct 1986. UT 91.3097 (1), Elk River Mile 29.7, 24 Oct 1986.

Other material not designated as types.—USNM 36670 (2) Shoal Creek, Florence [Lauderdale Co.], Alabama, 1884. A male taken with the holotype was frozen at UT for electrophoretic analysis; counts for this specimen are included in the tables. Two additional specimens, Elk River Mile 52.5, Giles Co., Tennessee, 14 Sep 1988, were frozen for electrophoretic analysis at UAIC, and are not included in the tables.

Diagnosis.—*Etheostoma wapiti* is a species of subgenus *Nothonotus* as defined by Page (1981). Within *Nothonotus, E. wapiti* belongs to the *E. maculatum* species group (Williams & Etnier, 1978), all of which have a few scales associated with the postorbital spot on the upper cheek (cheek completely naked in other *Nothonotus*). Within *Nothonotus, E. wapiti* differs from *acuticeps, aquali, jordani, juliae, maculatum, moorei, rubrum, sanguifluum,* and *tippecanoe* in having the combination of dark marginal

Table 3.—Frequency distribution, sample size, and means of selected fin-ray counts and vertebral counts in *Etheostoma wapiti, E. aquali, E. vulneratum,* and Elk River system *E. camurum.* Counts for *E. aquali* from Williams & Etnier (1978) and *E. vulneratum* from Zorach & Raney (1967). Vertebral counts for *E. camurum* not available.

	First dorsal fin							Second dorsal fin					
	11	12	13	14	15	n	x̄	11	12	13	14	n	x̄
E. wapiti		10	33	10		53	13.00	1	35	17		53	12.51
E. aquali		9	49	3		60	12.90	1	21	33	3	58	12.66
E. vulneratum	4	11	55	6	2	78	12.89	6	39	31		76	12.33
E. camurum	3	18	3			24	12.00	1	12	11		24	12.42

	Total dorsal-fin rays									Anal-fin soft rays					
	22	23	24	25	26	27	28	n	x̄	7	8	9	10	n	x̄
E. wapiti			8	27	16	2		53	25.23	8	35	8	1	52	8.04
E. aquali			4	24	25	5		58	25.54		2	42	15	59	9.22
E. vulneratum		1	7	43	21	3	1	76	25.28	16	50	9	1	76	7.93
E. camurum	1	2	9	10	2			24	24.42	8	15	1		24	7.71

	Pectoral-fin rays							Vertebrae					
	12	13	14	15	16	n	x̄	38	39	40	41	n	x̄
E. wapiti	2	23	28			53	13.49		4	5	1	10	39.70
E. aquali	1	25	31	2	1	60	13.63	2	27	1		30	38.97
E. vulneratum	2	23	47	4		76	13.70		6	25	1	32	39.84
E. camurum		6	16	2		24	13.83						

bands on median fins of both sexes, scales on the opercles, horizontal dark lines between scale rows on posterior half of body, a naked nape, and a completely scaled belly. Differs from *rufilineatum* in lacking large basicaudal pale spots, orange lips, and horizontal dark markings on the cheek. Differs from *bellum, camurum,* and *chlorobranchium* in lacking well defined pale submarginal bands on soft dorsal, caudal, and anal fins, and in having sexual dimorphism in soft dorsal and caudal fins throughout the year (pale yellow with small brown spots in female *wapiti*). Most similar to *E. vulneratum,* but differing from it (and all other *Nothonotus* except *acuticeps, chlorobranchium,* and occasional *maculatum*) in lacking red or orange on fins or body of nuptial males, and in having higher scale counts (Table 2). Other distinguishing characteristics of the species include moderately developed subocular bar, cheeks without wavy copper-colored lines.

In numerous adult and juvenile males a pale to yellowish submarginal band is present on the median fins that closely resembles that of male and female *E. camurum* and *E. chlorobranchium. Etheostoma camurum* and *E. wapiti* are sympatric in Elk River, and subadults and juveniles can be very difficult to separate. The former lacks any trace of a suborbital bar, never has scales associated with the postorbital dark spot, has a more blunt snout, and (Table 3) modally has 12 (vs. modally 13) dorsal spines.

Description.—*Etheostoma wapiti* is a moderately large species of the subgenus *Nothonotus,* the five adult (holotype and four paratopotypes) males from the type locality averaging 63.2 mm SL, the largest 70.8 mm SL. The three adult females from this collection are smaller, averaging 52.2 mm SL,

Table 4.—Characters useful in differentiating between five similar species in the *Etheostoma maculatum* species group.

Character	*E. wapiti*	*E. vulneratum*	*E. maculatum*	*E. sanguifluum*	*E. aquali*
Dark margins on anal, soft dorsal, and caudal fins	present	present	absent	absent	absent
Shape of caudal fin	truncate	truncate	rounded	rounded	rounded
Red on anal and pelvic fins, adult male	absent	absent	absent	present	present
Red on margin of spinous dorsal fin, adult male	absent	present	absent	present	present
Copper colored lines on cheek	absent	absent	absent	absent	present
Dark suborbital bar	present	present	often present	present	absent
Modal vertebral number	39 or 40	40	38	39	39
Mean lateral-line scales	61.65	57.87	60.91	56.53	62.21
Mean and (mode) of total dorsal-fin rays	25.23 (25)	25.28 (25)	24.65 (24–25)	24.97 (25)	25.53 (25–26)
Mean and (mode) of anal-fin soft rays	8.04 (8)	7.93 (8)	8.54 (8–9)	8.18 (8)	9.22 (9)

the largest 57.7 mm SL. Proportional measurements of the holotype and nine paratypes of *E. wapiti* are given in Table 1. The general body shape of *E. wapiti* is illustrated in Fig. 1.

Frequency distributions of scale, fin-ray, and vertebral counts for *E. wapiti* are given in Tables 2, 3. Body scaled except for the breast, prepectoral, and nape areas. Cheeks naked except for the typical presence of 2–5 embedded to partially exposed cycloid and/or ctenoid scales behind eye. Opercles scaled. Lateral-line complete with 55–69 ($\bar{x}$ = 61.6) scales. Transverse scales, anal-fin origin to first dorsal fin 15–20 ($\bar{x}$ = 18.4) and origin of second dorsal fin to anal fin 14–19 ($\bar{x}$ = 16.2). Caudal peduncle scale rows 21–25 ($\bar{x}$ = 22.8). Dorsal fin with 12–14 ($\bar{x}$ = 13.0) spines and 11–13 ($\bar{x}$ = 12.5) soft rays. Total dorsal fin elements 24–27 ($\bar{x}$ = 25.2). Anal fin with 2 spines and 7–9 ($\bar{x}$ = 8.0) soft rays. Pectoral-fin rays 12–14 ($\bar{x}$ = 13.5). Vertebrae 39–41 ($\bar{x}$ = 39.7). Branchiostegal rays 6-6, branchiostegal membranes separate. Frenum broad. Table 4 contains a summary of characters useful in differentiating between *Etheostoma aquali, E. maculatum, E. sanguifluum, E. vulneratum,* and *E. wapiti.*

Cephalic sensory canal pores are as follows: lateral canal pores 5–6, usually 5; preoperculomandibular canal pores 10–11, usually 10; infraorbital canal pores 7–9, usually 8; supraorbital canal pores 3; supratemporal canal pores 3; coronal pore single.

Coloration.—Following color description is based on the series collected at type locality on 7 Jun 1982. Body of males olive to grayish without red spots. Posterior half of body with 10–14 dark horizontal stripes between scale rows. Stripes are absent on belly and become pale dorsally and ventrally along caudal peduncle. Humeral scale black. Belly, breast, and prepectoral area grayish. Head grayish with distinct dark gray to black suborbital bar and postorbital spot. Iris dark with some yellow pigment. Cheeks uniform gray without chromatic markings. Gular area pale blue. Spinous dorsal fin dark gray with thin black marginal band and narrow pale yellow submarginal (marginal anteriorly) band. Soft dorsal fin gray with black marginal band and pale yellow submarginal band. Black marginal band on spinous and soft dorsal fins is wider and darker posteriad. Anal fin gray with narrow dark gray to black marginal band on posterior third of fin. Membrane between anal spines pale bluegreen. Caudal fin grayish with faint bluegreen base, pale yellow submarginal band, and black marginal band. Pelvic fins grayish with faint bluegreen membranes near base. Pectoral fins grayish with dusky margin posteriorly. Subadult males and unsexed juveniles collected during June and October 1986 had orange to red on caudal fin, narrow red margin and occasional red anterior interradial membranes of spinous dorsal fin, and occasional dirty red spots on posterior sides. Larger males from these collections lacked red or orange colors, except one October adult male had about ten obscure dirty red spots along posterior sides and reddish caudal fin. In the 13 adults (all males 43–62 mm SL) collected on 13 Sep 1988 and examined on 7 Oct, 1 of the smaller specimens had marginal red-orange on interradial membranes 1, 2, 4, and 6 of the spinous dorsal fin, and an additional 3 had marginal red-orange on membrane 1. Five of these had a few dirty red spots on the sides and five had orange on dorsal and ventral principal caudal fin rays in contrast to the pale yellow middle rays. The five largest males in this series (55–62 mm SL) were noticeably less colorful—none had red in the spinous dorsal fin, one had the red-orange caudal fin color described above, and four had pale yellow rays in either the soft dorsal or anal fin.

In females, coloration of head and body similar to that of males except paler. Spinous dorsal fin dusky gray, margin of first interradial membrane red. Soft dorsal and caudal fin pale yellow with dark brown speckles. Anal fin dusky gray, not speckled with brown. Median fins with narrow black marginal band. Pectoral and pelvic fins were colorless.

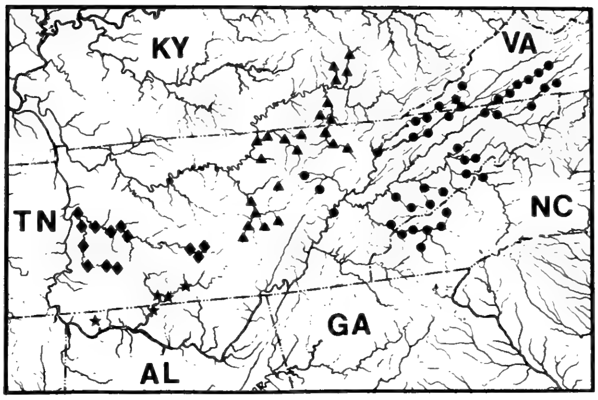

Fig. 2. Geographic distribution of *Etheostoma wapiti* (stars), *E. vulneratum* (dots), *E. aquali* (diamonds) and *E. sanguifluum* (triangles).

Distribution and habitat.—Etheostoma wapiti is known from the Elk River system in Tennessee and the Shoal Creek system in Alabama, both northern tributaries of the Tennessee River, along the southern portion of the Highland Rim physiographic province (Fig. 2). It was first collected in Shoal Creek in 1884 by C. H. Gilbert and J. Swain and subsequently reported (as *E. rufilineatum*) by Gilbert (1891). No habitat data were given and the only locality information was "Shoal Creek, Florence, Alabama." Shoal Creek, located east-northeast of Florence, Lauderdale Co., enters the Tennessee River about seven miles east of Florence. The lower portion is flooded by backwaters of Wilson Dam which extend upstream to the Lauderdale County Road 64 crossing. The two specimens of *E. wapiti* collected by Gilbert and Swain were most likely collected in the lower portion of Shoal Creek. While recent extensive efforts to collect *E. wapiti* in the unimpounded portion of Shoal Creek have been unsuccessful, it may still occur there since the remaining stream habitat appears to be in good condition and supports a large variety (50 species) of fishes.

The boulder darter is currently known from eight localities in the main channel of Elk River and from the lower reaches of two Elk River tributaries, Richland and Indian creeks. Adults have been found only in areas of boulder substrate, and we consider this strong circumstantial evidence that it shares egg-clumping reproductive habits with other members of the *maculatum* species group. In Elk River proper the most upstream record (two specimens, River Mile 89.7, Fayetteville, 1963, 1988) is in an area strongly influenced by cold water releases from Tims Ford Reservoir, completed in 1970. The 12 adult males and 1 juvenile from Elk River Mile 61.0, 13 Sep 1988, were collected in a high energy bend of the river where boulders eroded from an adjacent bluff provide habitat. Single juveniles from River Miles 40.8 and 41.0 are likely waifs that dispersed downstream from the Richland Creek population (mouth at River Mile 42.6). Elsewhere in Elk River, Tennessee, the population at the mouth of Indian Creek (River Mile 52.5) is apparently utilizing limestone slabs from a collapsed mill dam for spawning substrate; juveniles from this population enter lower Indian Creek, but no adults have been taken there and suitable spawning habitat is virtually absent. At River Mile 36.7, adults were taken in association with boulders from a former stone bridge. In Elk River, Alabama, natural outcrops of limestone occur above and below the Smith Hollow Road (Alabama Highway 127) bridge, and boulder darter populations are presumably rather continuous from River Mile 30.7 (ca. 400 m above bridge) downstream to about River Mile 29. At River Mile 28.1 (upstream end of Gallus Island) Elk River is impounded when Wheeler Reservoir is at full pool, and boulder darters were not collected.

Historically the boulder darter probably occurred in the main channel of the Tennessee River between Muscle Shoals and the mouth of the Elk River, a distance of approximately 45 miles. It is likely that it also occurred upstream from the mouth of Elk River and in the lower portion of other northern tributaries of the southern bend of the Tennessee River such as the Flint and Paint Rock rivers.

Conservation.—There are presently 55 known specimens of *Etheostoma wapiti.* Its habitat is difficult to sample with standard kick-seining methods which may account, at least in part, for its rarity. However, most of its potential habitat of deep, rocky, flowing pools in rivers and lower portions of large tributaries has been altered by impoundment, pollution, and siltation. It is likely that additional reproducing populations could be established in Elk River by merely providing suitable spawning substrate in areas with adequate current and good water quality. The restricted distribution of *E. wapiti* and loss of potential habitat in other large rivers of the area prompted the U.S. Fish and Wildlife Service to list it as an Endangered species (Biggins, 1988).

Etymology.—The species name, *wapiti,* is an American Indian name for the American elk and calls attention to the Elk River system, the only habitat presently known to support the species. The common name, boulder darter, is in reference to the habitat of adults.

We suggest the vernacular names of wounded darter for *E. vulneratum* and bloodfin darter for *E. sanguifluum.* These names are suggested by the meanings of the Latin *vulneratum* (=wounded) and *sanguifluum* (=flowing blood).

Phylogenetic analysis.—Following are characters utilized in assessing relationships within subgenus *Nothonotus,* with a brief survey of their distribution in outgroups and in *Nothonotus.* Our polarity judgements are included, but the PAUP program was run with polarity unfixed.

1. Horizontal dark lines on sides of body above and below lateral line. This character does not appear in any of the outgroups, and is essentially a subgeneric synapomorphy, secondarily lost only in *jordani* and *tippecanoe* as suspected autapomorphies.

2. The deep-bodied, slab-sided form of *Nothonotus* species (expressed as caudal peduncle depth divided by SL, data from Page

1981, and UT specimens) is a presumed synapomorphy for the subgenus. The caudal peduncle is slender in genus *Percina* (above ratio = 0.065–0.100) and in *Etheostoma* subgenera *Allohistium* (0.098) and *Litocara* (0.088–0.092). In subgenus *Oligocephalus* Page's (1981) values range from 0.089 to 0.116, with only *grahami* (0.115), *pottsi* (0.116), and *swaini* (0.112) having ratios higher than 0.108. Ten adults of both *grahami* and *swaini* from the UT collection were measured, and we get a value identical to Page's for *swaini,* but a value of 0.103 for *grahami.* In *Nothonotus,* Page's values range from 0.111 to 0.128. We rechecked three of Page's lower values with ten UT specimens, and get an identical value for *bellum* (0.114), but higher ratios for *jordani* (0.120 vs. 0.111) and *chlorobranchium* (0.133 vs. 0.118).

3. The darkened anterior interradial membranes of the spinous dorsal fin occur throughout subgenus *Nothonotus,* with similar pigment occurring in outgroups only in four of nine species of *Percina* subgenus *Alvordius* and in *Percina* (*Imostoma*) *shumardi.* We consider it to be a synapomorphy for *Nothonotus.*

4. Males with distinctive nuptial colors of blue, green, gray, or brown on breast. *Nothonotus* is often accorded the subgeneric vernacular of "bluebreast darters," and this presumed synapomorphy is consistent throughout the subgenus except in *juliae* (males darken on throat and breast, James & Taber 1986), and in *jordani* where green of the breast may extend to adjacent branchiostegal membranes and/or belly. In outgroups, nuptial breast color of this nature is absent (*Percina, Allohistium, Litocara*) or occasionally present only in *lepidum* (green branchiostegal membranes and breast) and *whipplei* (blue breast). In some other *Oligocephalus* (*caeruleum, radiosum, spectabile*) the orange-red of the branchiostegal membranes may extend onto the breast.

5. Naked nape. The consistent and excessive loss of nape squamation, typical of all *Nothonotus* except *juliae,* does not occur in outgroups, and is considered a synapomorphy uniting *Nothonotus* other than *juliae.* We interpret the scaly nape of *juliae* as symplesiomorphic with outgroups.

6. United gill membranes, an autapomorphy occurring in *juliae,* are absent from outgroups and from other *Nothonotus.*

7. Naked opercles. Autapomorphy, *acuticeps.* Opercles are consistently scaled in outgroups and other *Nothonotus.*

8. Marginal dark bands on caudal, soft dorsal, and anal fins. A presumed synapomorphy for *Nothonotus* except *juliae, acuticeps,* and *tippecanoe.* The character is absent in outgroups except in *E.* (*Oligocephalus*) *radiosum.* Characters 9, 10, 11, and 14 support our assuming this to be a shared reversal in *aquali, maculatum,* and *sanguifluum.* Character 10 suggests a possible homoplasy in *tippecanoe.*

9. Red spots on body of nuptial males. A synapomorphy for all species of *Nothonotus* except *acuticeps, juliae, tippecanoe,* and *wapiti.* Character 10 suggests a possible reversal in *tippecanoe.* Presence of red spots in juvenile males plus characters 10, 11, 14, and 15 indicate an obvious reversal in nuptial male *wapiti.* In outgroups, similar pigment occurs only in *E.* (*Oligocephalus*) *whipplei.*

10. Sexual dimorphism of fin pigment pattern throughout the year. The darkly speckled median fins of females of *rufilineatum, jordani, tippecanoe,* and the *maculatum* species group are markedly different from the pattern in males and persist throughout the year and in preservative. Except for *tippecanoe,* where it is tentatively treated as an autapomorphy, we consider it a synapomorphy for these species. In *Percina,* sexual pattern dimorphism in median fins is essentially absent (cannot be sexed in preservative) and sexual dichromatism is absent or weakly expressed during the breeding season except in subgenera *Ericosma, Hypohomus,* and *P.* (*Alvordius*) *crassa* and *roanoka.* In genus *Etheostoma* out-

groups and other *Nothonotus,* sexual dichromatism may be spectacular, especially during the breeding season, but these are alcohol-soluble pigments that are lost in preservative, again making accurate pattern-based sexing of museum specimens difficult or impossible.

11. Presence of scales on upper cheek, near postorbital spot. Although scaly cheeks are widespread in outgroups, and naked cheeks are routinely and, we suspect, correctly considered the derived condition in percids, we note that these scales, absent from *Nothonotus* except the *maculatum* species group (*aquali, maculatum, microlepidum, moorei, rubrum, sanguifluum, vulneratum, wapiti*) must be considered derived under the most parsimonius phylogenetic hypothesis.

12. Reduced belly squamation. A synapomorphy for *moorei* and *rubrum.* In other *Nothonotus* and in *Etheostoma* outgroups the belly is fully scaled or occasionally and variably with a small naked area anteriad. In genus *Percina,* a small portion of the anterior belly may be naked, or there may be seasonally or sexually variable naked areas corresponding to the position of the modified midventral scales.

13. Reduced vertebral number. A synapomorphy for *rubrum* and *moorei* and homoplastic in *juliae.* Modal vertebral counts as low as 36 also occur commonly in subgenus *Oligocephalus,* but not in other outgroups or in other *Nothonotus.*

14. Egg clumping. A synapomorphy known or inferred to be shared by six species of the *maculatum* species group, absent in outgroups, and absent in other *Nothonotus.* Voirs (1988) confirms that *E. moorei* buries its eggs in the gravel as is typical of other *Nothonotus.* It seems likely that *E. rubrum* will also be an egg-burier given the presence of adult males in gravel riffle areas throughout the breeding season.

15. Anal fin lacking bright colors in males, lacking spots in females. In genus *Percina,* anal fins of males lack bright colors except in nuptial *P.* (*Ericosma*) *evides* and *P.* (*Hypohomus*) *aurantiaca* where it is or may be iridescent blue. In genus *Etheostoma* outgroups, the anal fin of males is blue, green, or red, or combinations of these colors. In *Nothonotus,* the anal fin of males is orange, red, or green except in *vulneratum* and *wapiti.* In *wapiti,* a trace of iridescent blue was noted between the anal spines in nuptial males, but the remainder of the fin was gray, while in *vulneratum* the entire fin is gray. Failure of *vulneratum* and *wapiti* males to develop brightly colored anal fins during the breeding season (a presumed synapomorphy) implies significantly different courtship behavior. Correlated with this, the anal fin of female *vulneratum* and *wapiti* is unspotted, whereas in the remainder of the *maculatum* species group plus *jordani, rufilineatum,* and *tippecanoe,* females have the anal fin spotted (see character 10). While we do not feel justified in considering these as separate characters (anal fin pigmentation of males and females is likely to have the same genetic basis), our confidence in this character's validity as an indicator of the sister-species relationship between *vulneratum* and *wapiti* is certainly enhanced by its deviation from the *maculatum* species group norm in both sexes.

16. Absence (loss) of dark margins on soft-rayed median fins. In genus *Percina* and in *Etheostoma* subgenera *Allohistium* and *Litocara,* median fins other than the spinous dorsal lack dark margins. In *Oligocephalus,* a dark margin on the soft dorsal is frequently present, but only in *radiosum* do all three soft-rayed median fins have dark margins. In *Nothonotus,* darkly margined median fins are absent only in *acuticeps, juliae,* and *tippecanoe* (presumed symplesiomorphy), and as a presumed synapomorphy in *aquali, maculatum,* and *sanguifluum* of the *maculatum* species group. Other *Nothonotus* have dark margins on these fins consistently evident in males and often apparent in females.

17. Rounded caudal fin. This character is

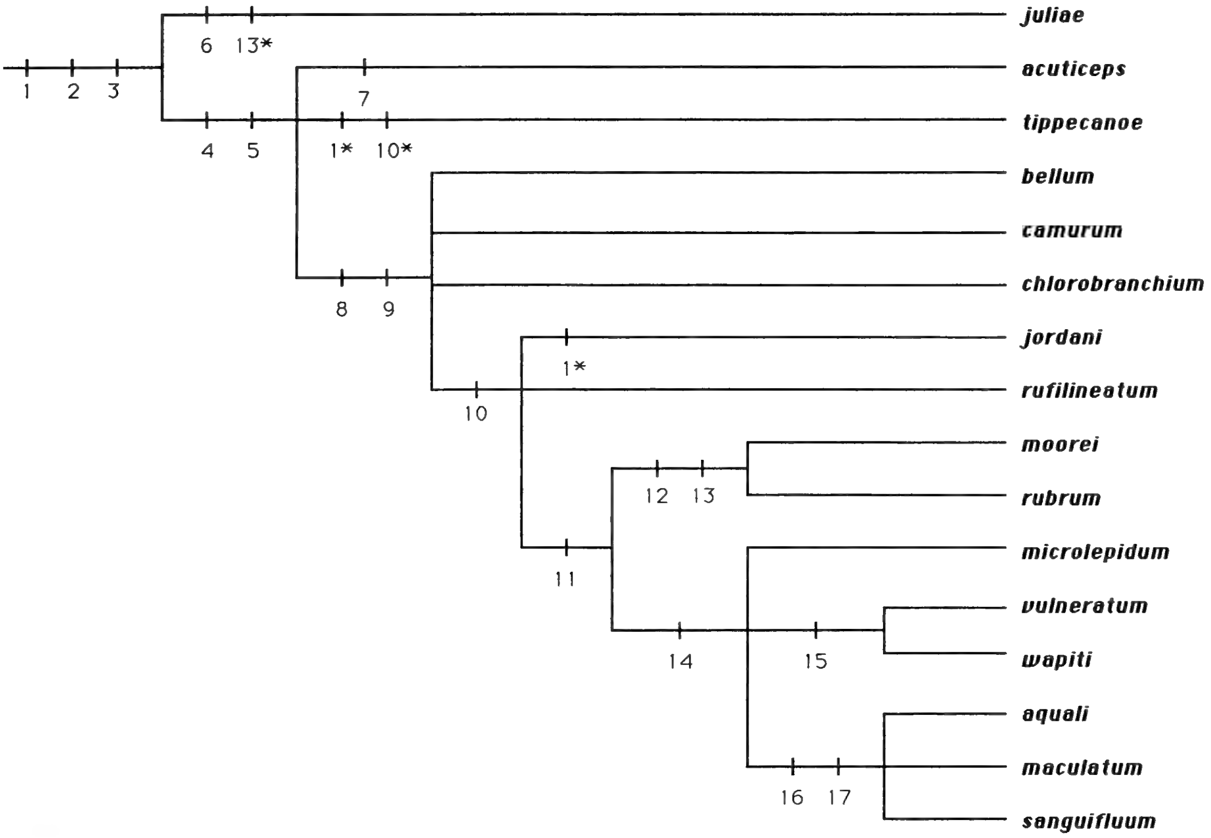

Fig. 3. Hypothesized phylogenetic relationships within subgenus *Nothonotus*. Characters 1–17 are discussed in the text. Asterisks indicate suspected homoplasies.

somewhat subjective, but we and Zorach & Raney (1967) find it useful, if somewhat variable, within the *maculatum* species group. The caudal fin is truncate to slightly forked in outgroups, and *Nothonotus* except for *aquali, maculatum,* and *sanguifluum.* We do note some sexual and size dimorphism in this character, with extremely large males of *vulneratum* occasionally having the caudal fin rounded, and occasional *sanguifluum,* especially females and smaller males, having the caudal fin truncate.

Discussion.—While characters 1–17 above are not sufficient to resolve relationships within subgenus *Nothonotus,* the concensus tree generated (Fig. 3, consistency index = 0.654) indicates that (1) *Nothonotus* is monophyletic; (2) *Etheostoma juliae* is sister to all other *Nothonotus*; (3) *Etheostoma acuticeps, E. tippecanoe,* and all other *Nothonotus* (except *juliae*) form an unresolved trichotomy; (4) although *E. bellum, E. camurum,* and *E. chlorobranchium* share all 17 characters analyzed, none is a synapomorphy for the three species, and their monophyly is not established; (5) the *E. maculatum* species group is monophyletic as are its branches of *moorei* + *rubrum, aquali* + *maculatum* + *sanguifluum,* and *vulneratum* + *wapiti*; (6) *Etheostoma moorei* and *E. rubrum* are sister to remaining members of the *maculatum* species group; and (7) *Etheostoma microlepidum* is included in an unresolved trichotomy with *aquali* + *maculatum* + *sanguifluum* and *vulneratum* + *wapiti.*

Prior to availability of sufficient material of *Etheostoma aquali* and *E. wapiti,* Zorach & Raney (1967) recognized *E. maculatum* as polytypic, including *E. m. sanguifluum* and *E. m. vulneratum.* They pointed out (p. 296) that "Three allopatric forms are recognized as subspecies, but might properly be considered as species." Our data indicate that *vulneratum* and *wapiti* are sister taxa and that *aquali* + *maculatum* + *sangui-*

fluum comprise a monophyletic branch, rendering their polytypic *E. maculatum* paraphyletic.

Our hypothesis concerning relationships between the taxa *aquali, maculatum, microlepidum, sanguifluum, vulneratum,* and *wapiti* differs from Page's (1985) hypothesized relationships between the species *aquali, maculatum, sanguifluum,* and *microlepidum* in which he treated *vulneratum* as a subspecies of *sanguifluum.* In his scheme, the polytypic *E. sanguifluum* and *E. aquali* are considered sister species based on the presumed synapomorphy of adult males with "two red spots at the front and one red spot at the rear" of the spinous dorsal fin. Although this pattern is distinctive, there is considerable variation within *aquali, sanguifluum,* and *vulneratum* in the extent of red margination, and a complete or nearly complete marginal band may be present. Marginal red pigment can occur in spinous dorsal fins of both *maculatum* and *wapiti* in subnuptial males (description, this paper, and Zorach & Raney 1967), but is absent in nuptial males. Red to orange margination in dorsal fins of male *Nothonotus* is variously expressed in all species except *acuticeps,* and perhaps *chlorobranchium,* and is often brighter anteriad. Since red margination of the spinous dorsal fin of males is present in subgenera *Allohistium* and *Litocara,* and often present although more submarginal in subgenus *Oligocephalus,* we treat this character as a symplesiomorphy within *Nothonotus,* and anterior and posterior concentration of this pigment, also variously expressed in several *Nothonotus,* is very suspect as a synapomorphy uniting *aquali, sanguifluum,* and *vulneratum.* Page's scheme conflicts with additional characters (rounded caudal fin, lack of bright colors in pelvic and anal fins of males, lack of dark spots on anal fin of females and lack of dark margins on median fins) that are supported by outgroup analysis as being synapomorphies within more derived *Nothonotus* species. We elevate *vulneratum* to species status based on our contention that *wapiti* and *vulneratum* are sister species, with either *microlepidum* or the unresolved trichotomy of *aquali, sanguifluum,* and *maculatum* as sister to that pair. The presumed synapomorphy uniting *wapiti* and *vulneratum* is secondary loss of bright colors in the anal and pelvic fins of adult males plus absence of spots in anal fin of females. The clade of *aquali, sanguifluum,* and *maculatum* share the presumed synapomorphies of rounded caudal fin and loss of dark margination on the median fins. Additional characters, whose polarity is difficult to evaluate, support the above relationships. Vertebrae are modally 40 in both *vulneratum* and *wapiti,* but modally 39 or fewer in other *Nothonotus* except *chlorobranchium* (39 or 40). High vertebral counts in *chlorobranchium* are likely related to its being the largest and most cold-adapted member of the subgenus, but neither *vulneratum* nor *wapiti* is larger than nor more tolerant of cold water than most other *Nothonotus* species. Mean anal fin ray counts are 7.93 and 8.04 for *vulneratum* and *wapiti,* respectively, but 8.18 or more for other egg-clumping *Nothonotus.* Simon et al. (1987) noted that egg diameter (2.8–3.1 mm) and hatchling length (8.3 mm SL) for *vulneratum* (treated as *E. sanguifluum vulneratum*) were larger than for other *Nothonotus* studied (egg diameter range 1.3–2.1 mm, hatchling length range 3.8–7.2 mm). *Etheostoma aquali* and *E. maculatum* were the only other members of the *maculatum* group included in their study. Our examination of egg diameter in gravid females of the *maculatum* species group (their data were based on fertilized, water-hardened eggs) confirms the large egg size in *E. vulneratum,* but the two available gravid females of *wapiti* had eggs within the range of sizes seen in the other species.

Zoogeography.—Dr. R. E. Jenkins (in litt.) has noted that dark marginal bands on median fins are less well developed in Clinch/Powell/Emory river *E. vulneratum* specimens than elsewhere. He has suggested that these might represent intergrades with *sanguifluum,* but this supposition demands a major headwater piracy event (members of the *maculatum* species group inhabit streams of order three or larger) between those systems and the Cumberland River drainage. Such a piracy has been alluded to (Ross 1971, Starnes et al. 1977), and similarities between fish faunas of the upper Cumberland River below the Falls and the adjacent Clinch/Powell/Emory systems certainly suggest such an event. Starnes & Etnier (1986) rethought and refuted this hypothesis based on the complete absence of geological evidence—Cumberland Gap was formed by faulting, and does not represent an extinct watercourse. They attribute faunal similarities to physiographic conditions (abundance of Silurian and/or Carboniferous sandstones in the watersheds and similar stream size and gradient) coupled with formerly more continuous distribution of ancestral forms throughout the Tennessee and Cumberland drainages. We accept this view as most likely, and any similarities between Cumberland *sanguifluum* and Clinch/Powell/Emory *vulneratum* are treated as homoplasies rather than as the result of recent contact. Assuming that main channel dispersal rather than headwater piracy has been responsible for present distribution, the ranges of *sanguifluum* and *vulneratum,* rather than abutting, are at maximum separation for the four taxa being considered (Fig. 2), with *aquali* and *wapiti* occupying geographically intermediate areas. These distributions and our proposed relationships of the four taxa conform nicely to the Starnes & Etnier (1986) hypothesis that, based on considerable geological evidence, the upper and middle portions of the Tennessee River drainage had a remote outlet from that of the present lower Tennessee and Duck river systems during the late Tertiary, and that the Tennessee achieved its present configuration in the Pleistocene. This development may have effected vicariance of the ancestral stock into a middle/upper Tennessee component (*vulneratum/wapiti* precursor) and a Duck/lower Tennessee/Cumberland river component (*aquali/sanguifluum* precursor). Further speciation into the four taxa considered here may be attributable to strict habitat requirements and physiographic fidelity of these darters (see discussion in Starnes & Etnier 1986). Since *vulneratum/wapiti* and *aquali/maculatum/sanguifluum* are supported as being monophyletic groups with *aquali* and *sanguifluum* likely sister species in the latter, a polytypic *maculatum* including *vulneratum* and/or *sanguifluum* would be paraphyletic. Monophyly could be retained by considering all five taxa as subspecies of a polytypic *Etheostoma maculatum,* a move we consider unwarranted. The unusual situation of two species (*aquali* and *wapiti*) evolving independently from two taxa that maintain their subspecies status (*sanguifluum* and *vulneratum,* respectively) could occur if (a) a founder effect were present, or (b) the allopatric ranges of *aquali* and *wapiti* presented drastically different selective pressures from those prevailing in the total range of *sanguifluum* and *vulneratum,* or (c) if the original subspecies continue to have or more recently have had a more continuous distribution than their vicariates. Since none of these, perhaps not exclusive, conditions appears likely, we are uncomfortable in accepting the derivation of two relatively distinct species (*aquali* and *wapiti*) from two different subspecies of a polytypic species.

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ELLERKELDIA, A JUNIOR SYNONYM OF *HYPOPLECTRODES,* WITH REDESCRIPTIONS OF THE TYPE SPECIES OF THE GENERA (PISCES: SERRANIDAE: ANTHIINAE)

William D. Anderson, Jr. and Phillip C. Heemstra

Abstract.—Characters that may prove useful in defining the serranid subfamily Anthiinae are briefly discussed, and a single synapomorphy, vertebral number, that unites the species of *Hypoplectrodes* is recognized. *Ellerkeldia* is considered a junior synonym of *Hypoplectrodes*; the relationships of *Hypoplectrodes* are discussed; the type species (*Plectropoma semicinctum* and *P. nigrorubrum*) of the two nominal genera are redescribed; and *Scopularia rubra* is demonstrated to be a junior synonym of *H. semicinctum. Hypoplectrodes semicinctum* is known from shallow waters off Juan Fernández and San Félix islands, and has been reported from Easter Island; *H. nigroruber* has been collected from shallow Pacific and Indian ocean waters off southeastern, southern, and southwestern Australia.

Some years ago, after examining the original descriptions of *Plectropoma semicinctum* and *Scopularia rubra,* one of us (PCH) concluded that the two species are synonymous. More recently the senior author examined the holotype of *P. semicinctum,* compared it with the original description of *S. rubra,* and arrived at the same conclusion. In view of the similarities of the descriptions in the literature of species of *Ellerkeldia* and of *Hypoplectrodes nigroruber,* the senior author examined the syntypes of *H. nigroruber* and determined that this species is congeneric with *P. semicinctum.* Because *H. nigroruber* is the type (and until now the only) species of *Hypoplectrodes* and *P. semicinctum* is the type species of *Ellerkeldia,* it follows that *Hypoplectrodes* and *Ellerkeldia* are subjective synonyms. The purposes of this paper are to redescribe *Hypoplectrodes nigroruber* and *H. semicinctum* and to document the assertions of synonymy made above.

Abbreviations and Methods

Institutional abbreviations are as listed in Leviton et al. (1985); ICZN denotes the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1985); SL signifies standard length and TL, total length.

Methods for making counts and measurements are those of Anderson & Heemstra (1980), except as noted below. Scales below the lateral line were counted obliquely, both in posterodorsal and anterodorsal directions from the origin of the anal fin (the posterodorsal direction is apparently the direction used by de Buen (1959) on *Scopularia rubra*).

Instead of scales in the lateral line, de Buen (1959) gave counts of scales in a longitudinal line. We interpret this to mean scales along the body in a mid-lateral line to base of caudal fin. It is difficult to get repeatable counts in a single longitudinal line of scales along the body; therefore our counts of "scales in a longitudinal line" are of oblique rows of scales along mid-body from cleithrum to base of caudal fin.

De Buen (1959) gave the lengths of specimens of *S. rubra* as total lengths, but the body proportions as percentages of standard length or head length. Based on the relationship of standard and total lengths in the specimens of *Hypoplectrodes semicinctum* examined, we have estimated the standard lengths of the types of *S. rubra*. Some of de Buen's measurements of *S. rubra* require interpretation; we have construed them as follows: height of body as greatest depth of body, width of body as greatest width of body, preorbital as length of snout, preventral as prepelvic length (premaxillary symphysis to origin of pelvic fin), and pectoral base as width of base of fin.

In the text some measurements are presented as quotients of the standard length, length of head, length of snout, or diameter of orbit. These quotients are rounded off to the nearest 0.05.

Anthiinae

Johnson (1983) defined the family Serranidae with respect to the Percichthyidae (sensu Gosline 1966) on the basis of three reductive specializations, and demonstrated that members of the Serranidae share at least one innovative specialization—thus demonstrating the monophyly of the family. Johnson (1983, 1988) followed Gosline (1966) in recognizing three subfamilies in the Serranidae, the Serraninae, Epinephelinae, and Anthiinae, but was able to define only the Epinephelinae on a character that can be interpreted as being uniquely derived. Olmi (1986) found a reductive character in the branchial skeleton that may prove to be a synapomorphy uniting the members of the Anthiinae. In all of the Atlantic and eastern Pacific species of anthiines that she examined and in all of the Indo-Pacific species for which she could obtain data the second epibranchial lacks a tooth plate, whereas it is present in all serranines and epinephelines observed in her study. She concluded that the absence of this tooth plate in the Anthiinae appears to be the derived condition in the Serranidae.

As pointed out by Johnson (1983) it is difficult to evaluate the importance of vertebral number in determining relationships among the Percoidei; nevertheless this character may ultimately prove useful in circumscribing the limits of the Anthiinae. Members of the Serraninae and Epinephelinae almost always have 24 vertebrae, but species of Anthiinae have 25 to 28, usually 26 (see section on relationships of *Hypoplectrodes*).

Until additional studies have been conducted the Anthiinae will continue to be an inadequately defined group. Despite this shortcoming the recognition of the Anthiinae as a distinct taxon will continue to serve a useful purpose because the concept anthiine unites a plethora of look-alike species that share at some level within the Serranidae uniquely derived characters.

Hypoplectrodes Gill, 1862

Hypoplectrodes Gill, 1862:236 (type species *Plectropoma nigrorubrum* Cuvier, 1828, by monotypy).

Gilbertia Jordan, 1891:346 (type species *Plectropoma semicinctum* Valenciennes, 1833, by original designation; preoccupied by *Gilbertia* Cossman, 1889, a genus of Mollusca).

Ellerkeldia Whitley, 1927:298 (type species *Plectropoma semicinctum* Valenciennes, 1833, by virtue of the facts that *Ellerkeldia* was proposed as a replacement name for *Gilbertia* Jordan, 1891, preoccupied by *Gilbertia* Cossman, 1889, and that a replacement name retains the type of the prior name [ICZN, Article 67h]; Whitley, 1927, incorrectly considered *Plectropoma annulatum* Günther, 1859, as the type species).

Scopularia de Buen, 1959:95 (type species *Scopularia rubra* de Buen, 1959 [=*Plectropoma semicinctum* Valenciennes, 1833], by original designation).

Diagnosis.—A genus of anthiine serranid fishes characterized by the following: 27 or 28 vertebrae (usually 27, very rarely 26), three predorsal bones, 17 principal caudal-fin rays (15 branched), one to three antrorse spines on preopercle, supramaxilla typically present, and maxilla without scales.

Gender.—Generic names such as *Hypoplectrodes,* with the suffix "–odes," are substantivated adjectives and are masculine (ICZN, Article 30b). Accordingly, adjectival specific names in combination with *Hypoplectrodes* must have the masculine termination (ICZN, Article 31b).

Species of Hypoplectrodes.—Allen & Moyer (1980:329) recognized six species in the genus *Ellerkeldia* (herein considered as species of *Hypoplectrodes*), presented a key for their identification, and stated that they "are confined to shallow temperate seas of New Zealand and southern Australia." They overlooked the type species of the genus *Ellerkeldia, Plectropoma semicinctum* (=*H. semicinctum*), from the eastern Pacific, presumably because Whitley (1927) mistakenly considered *Plectropoma annulatum* Günther, 1859, as the type species.

In addition to *H. semicinctum* and the type species of *Hypoplectrodes, H. nigroruber,* from waters off Australia, the other nominal species of the genus are: *H. annulatus* (Günther, 1859), *H. huntii* (Hector, 1875), *H. jamesoni* Ogilby, 1908, *H. maccullochi* (Whitley, 1929), *H. ruber* (Allen, 1976), which is in need of a replacement name because it is a junior secondary homonym of *Scopularia rubra* de Buen, 1959 [=*H. semicinctum*], and *H. wilsoni* (Allen & Moyer, 1980). John R. Paxton informed us (in litt., 23 Sep 1987) that he and Gerald R. Allen are in the process of revising *Ellerkeldia* (=*Hypoplectrodes*) and that they recognize two undescribed species of that genus from eastern Australia and New Zealand.

Relationships of Hypoplectrodes.—Randall (1980:102) considered *Ellerkeldia* (=*Hypoplectrodes*) to be "closely related to *Plectranthias*" Bleeker, 1873, and gave characters for separating the two genera. Heemstra & Anderson (1983) pointed out that Randall's characters would not distinguish these genera, but suggested that vertebral number might be useful (*Plectranthias* with 26 vertebrae, *Ellerkeldia* with 27). Doubt about the utility of vertebral number in distinguishing the genera is cast by the discovery of a new species of *Plectranthias* (*P. bilaticlavia*) from the Kermadec Islands off northern New Zealand by Paulin & Roberts (1987). The holotype of their new species has 27 vertebrae; the two paratypes (and only other specimens known) each have 26. Radiographs of the types of *P. bilaticlavia* revealed no indications of fusions or deformities of the vertebral columns. It is possible that a count of 27 vertebrae is rare for this species.

In order to evaluate the relationship of *Hypoplectrodes* with *Plectranthias,* detailed comparative studies of the species of the two genera are needed. This will be a formidable task because there are 10 species (8 with names, two undescribed) of *Hypoplectrodes* (see previous section) and 37 species of *Plectranthias* (Randall 1980, Fourmanoir & Rivaton 1980, Katayama & Masuda 1980, Fourmanoir 1982, Raj & Seeto 1983, Heemstra & Anderson 1983, Paulin & Roberts 1987). Further study will likely lead to the recognition at the generic level of one or more of the eight genera subsumed by Randall (1980) into *Plectranthias.* One of those yet to be resurrected genera is a logical candidate for recognition as the sister genus of *Hypoplectrodes.* A more precise estimation of these generic relationships is beyond the scope of this work.

In an attempt to provide a character analysis for *Hypoplectrodes* we consider other anthiines as the first outgroup, other serranids (serranines plus epinephelines) as the second, and other percoids as the third. In this analysis the only character whose states we feel confident in polarizing is vertebral number. Species of *Hypoplectrodes* have 27 or 28 vertebrae (one of 33 specimens of *H. maccullochi* examined with only 26; see Heemstra & Anderson 1983, and the generic diagnosis); other anthiines usually have 26 (one of three known specimens of *Plectranthias bilaticlavia* with 27, see above; *Giganthias immaculatus* Katayama, 1954, if indeed it is an anthiine, with 25; Boulenger 1895; Katayama 1959, 1960; Gosline 1966; Anderson & Heemstra 1980; Heemstra & Anderson 1983; Johnson 1983; our unpublished data). Other members of the Serranidae (serranines and epinephelines) almost always have 24 vertebrae (*Niphon,* a primitive epinepheline, with 30; *Pseudogramma* with 26, *Suttonia* with 26 or 27, *Aporops* with 27 or 28—these last three genera being highly derived grammistin epinephelines; Boulenger 1895; Katayama 1959, 1960; Gosline 1966; Johnson 1983; Leis & Rennis 1983; Carole C. Baldwin, pers. comm.). Forty-five of the 91 groups of percoids listed by Johnson (1984, Table 120) have 24 or 25 vertebrae lending support to Gosline's (1968, 1971) assertion that "the basal percoid number" is 24 or 25. In view of the preceding we interpret 24 or 25 as the most primitive character state for vertebral number in the Serranidae and 26, 27, and 28 as progressively more derived states. Accordingly, then, we consider the number of vertebrae (27 or 28) as a synapomorphy uniting the species of *Hypoplectrodes.*

Hypoplectrodes nigroruber and *H. semicinctum*

Because *Hypoplectrodes nigroruber* and *H. semicinctum* are very similar, it is appropriate to characterize those two species under a single heading and then to elaborate as necessary under the respective species accounts.

Single dorsal fin (not divided to base between spinous- and soft-rayed parts). Margin of anal fin broadly rounded to squared off posteriorly. Second spine of anal fin more robust than first or third, considerably longer than first, usually slightly longer than third. Pectoral fin symmetrical, middle rays longest; dorsalmost ray unbranched, the others usually branched. Pelvic-fin rays I, 5; pelvic fin inserted at vertical from base of pectoral fin, falling short of anal fin. Caudal fin truncate; principal rays 9 + 8; branched rays 8 + 7. Procurrent spur (Johnson 1975) absent. Parhypural and five autogenous hypurals present; epurals three. No dorsal trisegmental pterygiophores. Formula for predorsal bones, anterior neural spines, and anterior dorsal pterygiophores 0/0+0/2/1+1/.

Scales ctenoid, resembling those of serranine serranids (i.e., with rows of ctenial bases [Hughes 1981] present proximal to marginal cteni); no secondary squamation. Most of head covered with scales; dorsum and lateral aspect of snout, maxilla, supramaxilla, lower jaw, membranes between branchiostegals, and most of branchiostegals without scales; gular region usually without scales; squamation variously developed on interopercle, but usually confined to posterior part. No axillary process at base of pelvic fin. Squamation well developed on bases of all fins and continuing for some distance onto fins. Lateral line complete, extending to at least base of caudal fin (running parallel to dorsal body contour below dorsal fin, curving to near midlateral axis of body on caudal peduncle).

Supramaxilla present. Premaxillae protrusile. Posterodorsal border of maxilla not covered by elements of circumorbital series when mouth closed. Mouth terminal. Posterior margin of preopercle serrate; one to three antrorse spines on preopercle (one spine usually at angle or on ventral margin near angle, other spine(s) on ventral margin). Posterior margin of bony opercle with three spinous processes, middle one best de-

Fig. 1. Lectotype of *Plectropoma nigrorubrum,* MNHN 7776, 189 mm SL; Western Australia.

veloped. Distal margins of interopercle and subopercle usually smooth, occasionally with a few serrae or slightly roughened. On each side of snout, two closely set nares near eye. Snout usually longer than diameter of orbit. Diameter of bony orbit considerably greater than bony interorbital width. Branchiostegals seven. Gill arches four, with a slit behind fourth. Well developed gillrakers rather short (longest gillrakers usually shorter than longest gill filaments), anterior lower-limb rakers and most of upper-limb rakers rudimentary. Vomer and palatines with teeth; vomerine tooth patch chevron shaped, without a backward prolongation; palatine teeth in a longitudinal band. No teeth on tongue or pterygoids.

Hypoplectrodes nigroruber (Cuvier, 1828)
Figs. 1, 2; Tables 1–5

Plectropoma nigrorubrum Cuvier, 1828:402 (original description; lectotype, herein designated, MNHN 7776, 189 mm SL; type locality Port du Roi Georges [=King George Sound, Western Australia]).

Diagnosis.—This species appears to be distinguishable from all other species of *Hypoplectrodes* in morphology of the lateral-line scales (lateral-line tubes reaching posterior borders of scales; tubes of anterior lateral-line scales highly branched, becoming less so posteriorly, tubes of posteriormost scales bifurcate or unbranched) and in having an area of very small scales (on dorsum and dorsolateral part of body dorsal to lateral line) beginning at anterior end of dorsal fin and extending anteriorly to become continuous with scaly regions of head. Posteroventral corner of maxilla usually without prominent extension. Ventral margin of preopercle with one to three, usually two, antrorse spines; spines sometimes covered by skin. Vertebrae usually 27 (10 precaudal + 17 caudal), occasionally 28 (10 + 18). Pleural ribs on vertebrae 3 through 10 (3–11 in one of 15 specimens). Dorsal fin rays X, 16 to 18. Anal fin rays III, 8. Pectoral-fin rays 13 to 15, usually 14. Gillrakers, including rudiments, on first gill arch 5 or 6 + 12 to 16—total 17 to 22; developed gillrakers on lower limb 5 to 7. Tubed lateral-line scales 55 to 65, most frequently 57 to 63. Scales from anal-fin origin to lateral line 19 to 23 (counted posterodorsally), 23 to 28 (counted anterodorsally). Scales on cheek quite small; rows of cheek scales very difficult to count; number of cheek scale rows

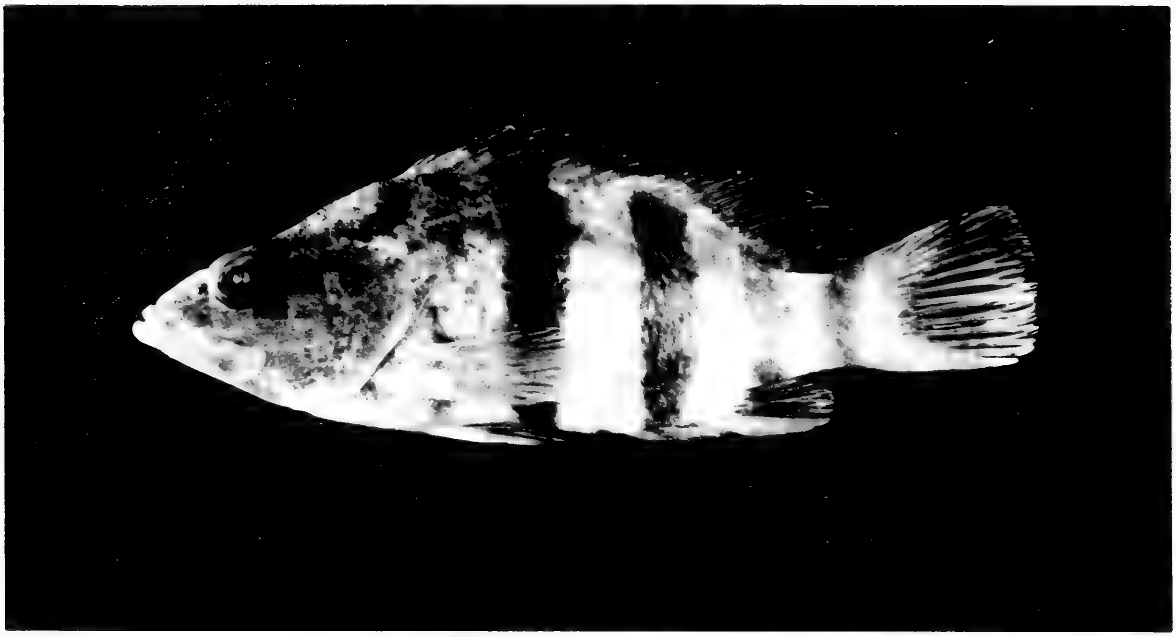

Fig. 2. *Hypoplectrodes nigroruber*, AMNH 31307, 114 mm SL; Western Australia.

ca. 21 to ca. 29, usually ca. 22 to ca. 26. Pseudobranch with 26 to 36 filaments, tending to increase in number with increase in SL. Length of second anal spine 10.3 to 15.1% SL. Body encircled by four darkly pigmented bands.

Description.—Characters included in the combined description of *H. nigroruber* and *H. semicinctum* and those presented in the species diagnosis form part of the species description. Frequency distributions for a number of meristic traits are in Tables 1 to 4; morphometric data appear in Table 5.

Procurrent caudal-fin rays 8 to 10 (usually 8) dorsally, 6 to 9 (usually 8) ventrally. Epipleural ribs associated with first 9 or 10 vertebrae (infrequently with 10th). Anal trisegmental pterygiophores 0 to 5 (most frequently 4). Rows of scales between lateral line and mid-base of spinous dorsal fin 3 or 4 (usually 3). Scales from dorsal-fin origin to lateral line 4 to 7 (usually 5 or 6). Circum-caudal-peduncle scales 30 to 34 (most frequently 30 or 31).

Depth of body (at origin of dorsal fin) 2.80 to 3.15, length of head 2.25 to 2.45 in SL. Horizontal diameter of bony orbit 4.40 to 6.70 in length of head, 1.10 to 1.95 in length of snout. Bony interorbital width 13.20 to 19.45 in length of head, 2.30 to 4.40 in diameter of bony orbit. Lower jaw exceeding upper when mouth closed. Maxilla reaching vertical through posterior part of orbit to slightly beyond orbit. Anterior naris at distal end of short tube; posterior border of tube produced into a flap which reaches or falls just short of posterior naris when reflected. Premaxilla with wide band of small conical teeth; band narrower posteriorly; posterior teeth at anterior end of band (near

Table 1.—Frequency distributions of numbers of fin rays in two species of *Hypoplectrodes*. Separate counts from both left and right pectoral fins included. Counts of name-bearing types are indicated by asterisks.

	Dorsal soft rays								Anal soft rays			Pectoral-fin rays						
Species	16	17	18	19	20	21	22	$\bar{x}$	7	8	9	13	14	15	16	17	18	$\bar{x}$
H. nigroruber	2	10*	4					17.12		16*		1	29*	1				14.00
H. semicinctum				6*	15	16	1	20.32	1	36*	1			1	16*	57	2	16.79

Table 2.—Frequency distributions of numbers of gillrakers on first gill arch in two species of *Hypoplectrodes*. Counts of name-bearing types are indicated by asterisks.

	Upper limb							
	Developed	Rudimentary			Sum (dev. + rud.)			
Species	1	3	4	5	4	5	6	$\bar{x}$
H. nigroruber	16*		6*	10		6*	10	5.62
H. semicinctum	38*	2	28	8*	2	28	8*	5.16

	Lower limb																			
	Developed						Rudimentary									Sum (dev. + rud.)					
Species	5	6	7	8	9	$\bar{x}$	4	5	6	7	8	9	10	11	$\bar{x}$	12	13	14	15	16	$\bar{x}$
H. nigroruber	2	12*	2			6.00			4	6	4*	—	1	1	7.44	4	6	3*	1	2	13.44
H. semicinctum				21	17*	8.45	17	19*	2						4.61	4	28	6*			13.05

	Total (upper limb + lower limb)						
Species	17	18	19	20	21	22	$\bar{x}$
H. nigroruber	2	4	6*	1	1	2	19.06
H. semicinctum	6	21	8	3*			18.21

Table 3.—Frequency distributions of numbers of tubed lateral-line scales in two species of *Hypoplectrodes*. Counts of name-bearing types are indicated by asterisks.

Species	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	$\bar{x}$
H. nigroruber								1	—	2	1	4*	—	4	2	1	—	1	59.94
H. semicinctum	5	8	12*	8	3	—	—	2											50.16

symphysis) larger and recurved; usually one to a few teeth at anterior end of jaw enlarged into small canines; no teeth at symphysis. Dentary with band of small conical teeth; band considerably widened near symphysis; one to a few small canines present about one-third way from symphysis to posterior end of band; teeth at anterior end of band near symphysis mostly recurved—more posterior ones somewhat enlarged; one to a few small canines at anterior end of jaw; no teeth at symphysis. Villiform to small conical teeth on vomer and palatines. Fourth, fifth, or sixth (usually fourth or fifth) dorsal spine longest. First anal spine 1.50 to 2.05 in second anal spine. Pectoral fin reaching vertical through anterior part of anal fin or pectoral fin appreciably shorter.

Coloration.—In alcohol head mottled dorsally and laterally, lighter ventrally. Dark bar just anterior to dorsal fin descending from dorsal contour to terminate where opercle joins body dorsally. Rather weakly pigmented bar ventral to anterior part of spinous dorsal fin which descends for variable distances ventrally. Four darkly pigmented bands, usually narrower than lightly pigmented interspaces, encircling body: anteriormost ventral to middle of spinous dorsal fin, second extending from anterior end of soft dorsal fin to anterior end of anal fin, third ventral to posterior end of soft dorsal fin, posteriormost on caudal peduncle; area in anteriormost band just ventral to lateral line more heavily pigmented. Fins without distinctive pigmentation except where weakly pigmented bar and three anteriormost bands encroach upon dorsal and anal fins. Cuvier (1828) wrote that the body is a very vivid red-orange and is crossed by five black bands: the first is faint and originates beneath the first rays of the dorsal; the other four are very dark; the last encircles the base of the tail. Castelnau (1875:8) stated that this species has "five broad transverse black bands on a reddish ground colour."

Distribution.—We have examined specimens collected in Pacific and Indian ocean waters of Australia off New South Wales, Victoria, South Australia, and Western Australia. Scott (1979) reported two specimens from Tasmanian waters (one from off the northeastern coast in Banks Strait; the other off the southwestern coast, off Port Davey). Depths of capture are available for only a few collections; they range from 3.5 to 15 m.

Gender.—The only published spelling that we have seen for the specific name in combination with *Hypoplectrodes* is *nigrorubrum.* The compound *nigrorubrum* is an adjective and in association with *Hypoplectrodes* (which is masculine, see section on gender of *Hypoplectrodes*) must have the

Table 4.—Frequency distributions of numbers of pseudobranchial filaments in two species of *Hypoplectrodes*. Counts of name-bearing types are indicated by asterisks.

Species	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
H. nigroruber													2	2	1	2	—	2	3*	1	—	—	2
H. semicinctum	2	—	—	—	1	2	2	5	5	5	4	4*	3	2	1								

Table 5.—Data on morphometric characters for two species of *Hypoplectrodes*. Standard lengths are in mm; other measurements, in percentages of standard length.

	H. nigroruber		*H. semicinctum*	
Character	n	Range	n	Range
Standard length	15	84.8–203	17	77.9–177
Head, length	15	40.4–44.3	17	38.6–45.1
Snout, length	14	9.4–12.7	17	9.6–13.4
Orbit, diameter	15	6.6–9.3	17	6.5–10.0
Postorbital length of head	15	21.0–26.8	17	21.3–23.7
Upper jaw, length	15	16.1–19.3	17	17.7–19.8
Maxilla, width	15	4.9–6.4	17	5.5–6.7
Interorbital width	15	2.1–3.3	17	2.9–3.8
Body, depth at origin of dorsal fin	15	32.0–35.5	17	32.9–37.1
Predorsal length	15	37.4–41.0	17	38.2–43.9
Preanal length	15	62.6–73.1	17	65.4–73.0
Caudal peduncle, length	15	18.8–22.0	17	18.7–21.7
Caudal peduncle, depth	15	11.0–13.0	17	10.0–12.4
Pectoral fin, length	15	25.7–31.5	17	27.0–34.2
Pelvic fin, length	15	19.7–22.8	17	21.0–25.8
Anal fin, depressed length	15	25.4–30.9	17	28.7–32.2
Upper caudal-fin lobe, length	12	19.2–25.0	16	20.9–25.3
Lower caudal-fin lobe, length	14	19.6–25.0	17	20.9–25.7
Third dorsal spine, length	13	12.3–>15.4	17	11.9–>14.6
Fourth dorsal spine, length	15	13.9–17.2	17	13.1–17.3
Longest dorsal spine, length	15	13.9–18.2	16	13.5–17.6
First anal spine, length	15	5.8–8.3	16	7.3–9.8
Second anal spine, length	15	10.3–15.1	17	14.6–19.7
Third anal spine, length	14	9.5–14.0	16	12.3–17.1

masculine termination (ICZN, Article 31b); consequently the correct binomen is *Hypoplectrodes nigroruber.*

Remarks.—Through the courtesy of M. L. Bauchot we have examined the two syntypes (MNHN 7776) of *Plectropoma nigrorubrum.* Both are in poor condition, but the larger is in a better state of preservation. We hereby designate as the lectotype of *Plectropoma nigrorubrum* Cuvier, 1828, the syntype of 189 mm SL, which retains MNHN 7776 as its catalog number; the paralectotype (142 mm SL) has been assigned a new number (MNHN 1988-799).

Material examined.—Sixteen specimens, 85 to 203 mm SL.

Lectotype: MNHN 7776 (189 mm SL); King George Sound, Western Australia; J. Quoy & P. Gaimard.

Paralectotype: MNHN 1988-799 (142 mm SL); same data as for lectotype.

Other material: USNM 42015 (one specimen, 193 mm SL), Port Jackson, New South Wales; USNM 42019 (1, 198), Port Jackson, New South Wales; CAS-SU 9189 (1, 203), Maroubra, New South Wales; CAS-SU 20797 (1, 199), Port Hacking, New South Wales; NMV A2554 (1, 174), Cape Wellington, Wilson's Promontory, Victoria, 39°4.1′S, 146°28.6′E, <10 m, R. Kuiter and M. McDonald, 9 Feb 1982; NMV A2588 (1, 163), western shore of Brown Head, Wilson's Promontory, Victoria, 39°2.7′S, 146°28.3′E, 15 m, T. Cochrane, R. Kuiter, and M. Larsen, 9 Feb 1982; NMV A3007 (1, 134), northern shore of Horn Point, Wilson's Promontory, Victoria, 39°1.6′S, 146°28.2′E, <10 m, R. Kuiter and M.

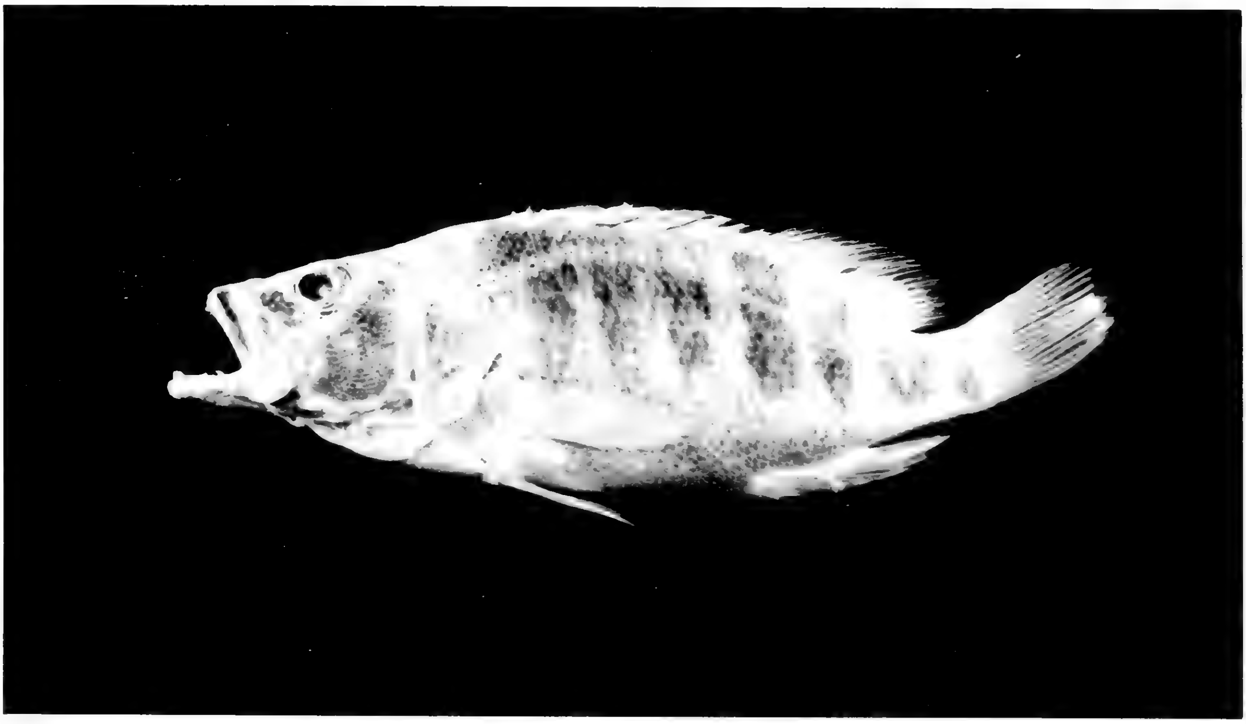

Fig. 3. Holotype of *Plectropoma semicinctum,* MNHN 7777, 146 mm SL; Juan Fernández Islands.

McDonald, 9 Feb 1982; USNM 177114 (1, 157), around Kangaroo Island and St. Stephens Bay, South Australia, Howard, Mar–Apr 1952; NMV A289 (1, 86), Cape Cassini, Kangaroo Island, South Australia, 35°35′S, 137°19′E, W. Gosline and J. Glover, 17 Aug 1966; AMNH 31307 (4, 85–128), northeast and southwest sides of North Point, south of Boulder Hill, Western Australia, ca. 34°56′S, ca. 118°13′E, 3.5 m, Nelson, Butler, and Rosen, 14 Mar 1969; NMV A5061 (1, 167), Champion Bay, Western Australia, 28°46′S, 114°36′E.

Hypoplectrodes semicinctum
(Valenciennes, 1833)
Figs. 3–5; Tables 1–6

Plectropoma semicinctum Valenciennes, 1833:442 (original description; holotype MNHN 7777, 146 mm SL; type locality Juan Fernández Islands, eastern Pacific Ocean).

Scopularia rubra de Buen, 1959:95 (original description and illustration; holotype EBMC 123–124,174 mm TL, apparently lost; type locality Cumberland Bay, Más a Tierra Island, Juan Fernández Islands, eastern Pacific Ocean).

Diagnosis.—Lateral-line tubes reaching posterior borders of scales; tubes of anterior lateral-line scales bifurcate; those of posterior scales unbranched. Scales on body anterior to dorsal fin not greatly reduced in size (except one of 38 specimens with small area of reduced scales adjacent to anterior end of dorsal fin). Posteroventral corner of maxilla usually with prominent extension. Ventral margin of preopercle with two or three, usually three, antrorse spines; spines frequently covered by skin. Vertebrae 27 (10 precaudal + 17 caudal). Pleural ribs on vertebrae 3 through 10. Dorsal fin rays X, 19 to 22. Anal fin rays III, seven to nine (usually eight). Pectoral-fin rays 15 to 18 (usually 16 or 17). Gillrakers, including rudiments, on first gill arch 4 to 6 + 12 to 14—total 17 to 20; developed gillrakers on lower limb 8 or 9. Tubed lateral-line scales 48 to 55, most frequently 48 to 51. Scales from anal-fin origin to lateral line 16 to 20

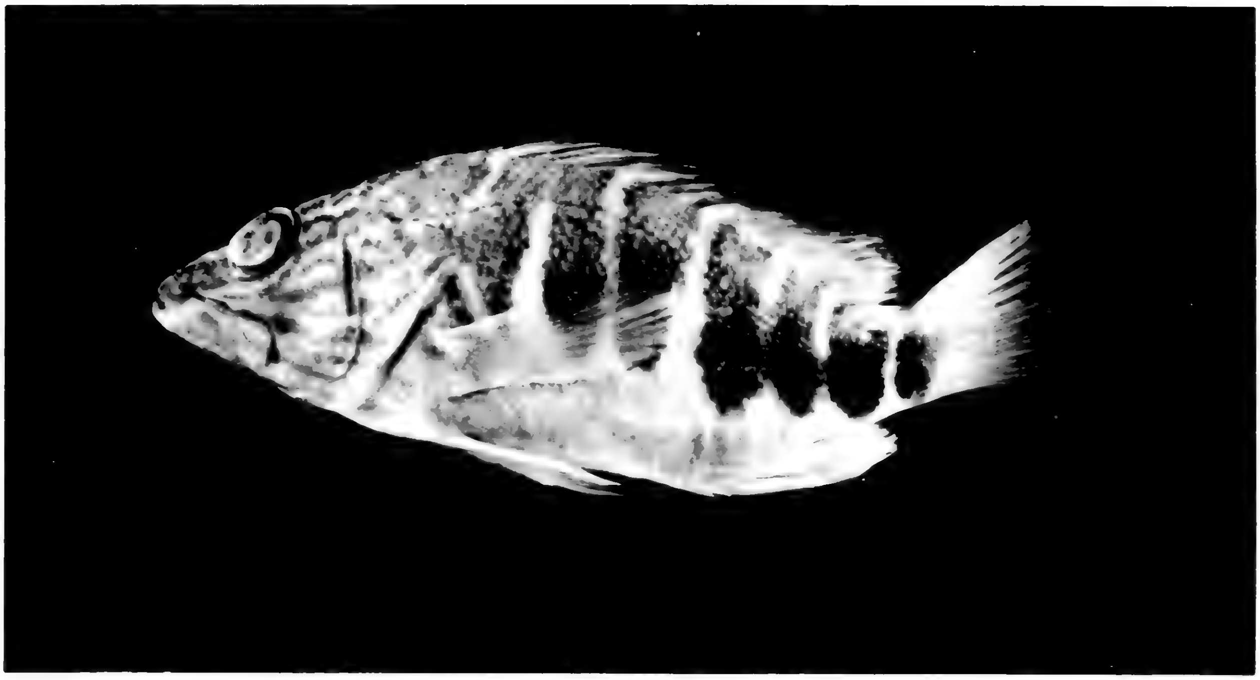

Fig. 4. *Hypoplectrodes semicinctum,* MCZ 46165, 108 mm SL; Juan Fernández Islands.

(counted posterodorsally), 19 to 24 (counted anterodorsally). Rows of cheek scales 14 to 19. Pseudobranch with 14 to 28 filaments, tending to increase in number with increase in SL. Length of second anal spine 14.6 to 19.7% SL. Body usually with 9 darkly pigmented bars (including one on nape); bars wider than lightly pigmented interspaces.

Description.—Characters included in the combined description of *H. nigroruber* and *H. semicinctum* and those presented in the species diagnosis form part of the species description. Frequency distributions for a number of meristic traits are in Tables 1 to 4; morphometric data appear in Table 5.

Procurrent caudal-fin rays 8 to 10 (very rarely 10) dorsally, 6 to 9 (usually 7 or 8) ventrally. Epipleural ribs associated with first 9 or 10 vertebrae (usually first 9). Anal trisegmental pterygiophores 0 to 3 (most frequently 1). Rows of scales between lateral

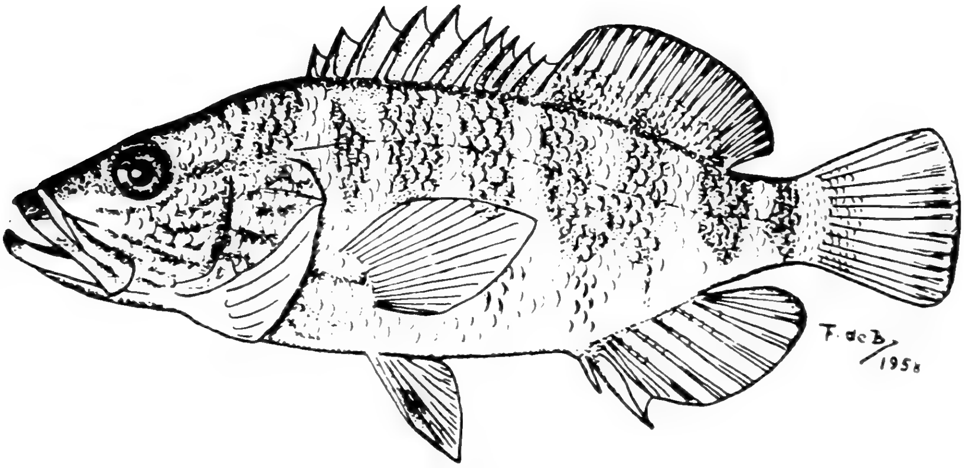

Fig. 5. Holotype of *Scopularia rubra,* EBMC 123-124, 174 mm TL (from de Buen, 1959); Juan Fernández Islands.

Table 6.—Comparisons of data on *Hypoplectrodes semicinctum* and data from de Buen (1959) on holotype and paratype of *Scopularia rubra* (EBMC 123–124). Standard lengths and total lengths are in mm; other measurements in percentages of standard length (% SL) or percentages of head length (% HL). L = left; R = right; ruds. = rudimentary gillrakers; est. = standard lengths estimated (see text); > = slight damage to caudal fin.

	H. semicinctum		*S. rubra*
Character	Range	Holotype	Holotype and paratype
Dorsal-fin rays	X, 19–22	X, 19	X, 20
Anal-fin rays	III, 7–9	III, 8	III, 8
Pectoral-fin rays	15–18	16	16
Gillrakers:			
Total	17–20	20	16
Upper limb	4–6 (1+3–5 ruds.)	6 (1+5 ruds.)	5 (1+4 ruds.)
Lower limb	12–14 (8 or 9+4–6 ruds.)	14 (9+5 ruds.)	11 (8+3 ruds.)
Lateral-line scales	48–55	50 (L), 49 (R)	—
Scales in longitudinal line (see text)	—	ca. 50 (L), ca. 53 (R)	49–52
Scales above lateral line	5–7	6	5 or 6
Scales below lateral line (see text)	16–20	ca. 16	14 or 15
Standard length	77.9–177	146	143 and 107 (est.)
Total length	97.3–214	>179	174 and 131
	% SL	% SL	% SL
Head, length	38.6–45.1	38.6	39.3–41.5
Body, depth (greatest)	33.3–38.8	33.7	34.5–34.9
Body, width (greatest)	15.3–20.5	15.9	18.6–18.8
Predorsal length	38.2–43.9	38.2	40.0–41.5
Preanal length	65.4–73.0	71.2	72.4–76.4
Prepelvic length	37.5–45.8	44.9	46.2–52.8
Dorsal-fin base	51.9–58.1	53.8	50.0–53.8
	% HL	% HL	% HL
Snout, length	23.1–31.1	27.8	34.0–36.5
Orbit, diameter	14.9–24.0	19.9	17.5–22.7
Postorbital length of head	50.9–55.6	55.1	50.0–52.2
Interorbital width	6.8–9.6	9.6	11.3–14.0
Caudal peduncle, depth	23.2–29.8	27.0	29.7–29.8
Pectoral-fin base, width	16.8–21.3	20.2	20.4–22.8
Pectoral fin, length	65.7–80.6	70.9	63.6–64.9
Pelvic fin, length	50.4–61.8	56.4	43.8–50.0

line and mid-base of spinous dorsal fin 3 or 4 (most frequently 4). Scales from dorsal-fin origin to lateral line 5 to 7 (most frequently 6). Circum-caudal-peduncle scales 27 to 32 (usually 28 to 30).

Depth of body (at origin of dorsal fin) 2.70 to 3.05, length of head 2.20 to 2.60 in SL. Horizontal diameter of bony orbit 4.15 to 6.75 in length of head, 0.95 to 2.05 in length of snout. Bony interorbital width 10.45 to 14.75 in length of head, 1.70 to 3.30 in diameter of bony orbit. Jaws nearly equal or lower jaw exceeding upper when mouth closed. Maxilla usually falling short of vertical through posterior margin of orbit. Anterior naris at distal end of tube; posterior border of tube elongated slightly, but falling short of posterior naris when reflected. Premaxilla with band of small conical teeth; band expanded anteriorly; posterior teeth in expanded part of band (adjacent to symphysis) enlarged and posteriorly directed; one or two canines at anterior end of jaw; no teeth at symphysis. Dentary with band of small conical teeth; band somewhat expanded adjacent to symphysis; one to three canines at about middle of band; numerous enlarged posteriorly directed conical teeth at anterior end of band near symphysis; one or two canine teeth (may be exserted) at anterior end of jaw; no teeth at symphysis. Small conical teeth on vomer and palatines. Fourth, fifth, or sixth (usually fifth) dorsal spine longest. First anal spine 1.75 to 2.25 in second anal spine. Pectoral fin usually reaching vertical through anterior part of anal fin.

Coloration.—In alcohol dorsum of head mostly darkly mottled; cheek and opercular series with several mostly horizontal stripes, narrower than lighter interspaces. Body usually with nine darkly pigmented bars; bars evenly spaced, wider than lightly pigmented interspaces; anteriormost bar on nape (saddle-like, extending over dorsum to join bar from other side); second bar beginning on nape and beneath anterior part of spinous dorsal fin; third through fifth bars beneath spinous dorsal fin; sixth through eighth bars beneath soft dorsal fin; eighth bar also extending onto and over caudal peduncle to become continuous with corresponding bar from other side; eighth bar surrounding small lightly pigmented area dorsally just posterior to base of soft dorsal fin; ninth bar on caudal peduncle; second through fifth bars usually extending about 60 to 70% of distance from dorsum to ventral midline (on specimens more than ca. 100 mm SL; on smaller specimens these bars may extend further ventrally); on many specimens sixth through eighth bars becoming very narrow ventrally, sometimes reaching anal fin or ventral border of caudal peduncle (eighth); very frequently eighth and ninth bars becoming narrowly confluent with corresponding bars from other side; bars frequently showing various anastomoses, often bars three and four, four and five, and six and seven uniting broadly. Fins mostly straw colored except where dark bars extend onto dorsal and anal fins.

Valenciennes (1833) described the coloration of the holotype of *Plectropoma semicinctum.* He wrote that the colors of this fish are a beautiful vermilion red, traversed by eight half bands of a bright red brown, that descend on the back and stop on the middle of the sides, so as to form half belts on the sides. Only the last almost encircles the entire tail. Some paler and oblique brown bars cross the cheeks, and form on the opercle indistinct rivulations. The dorsal and caudal are reddish. The pectorals, ventrals, and anal are olive, mixed with the red that forms the general background color. De Buen (1959) stated that *Scopularia rubra* is red with black bands.

Distribution.—We have examined specimens of *H. semicinctum* collected in the eastern South Pacific off the Juan Fernández Islands and San Félix Island in shallow waters with a maximum depth of 20 m. Yáñez-Arancibia (1975) illustrated a specimen identified as *Scopularia rubra* that was collected at Easter Island. This drawing is a good representation of *H. semicinctum*; accordingly, then, it would appear that *H. semicinctum* can be considered as reliably reported from Easter Island. Randall & Cea Egaña (1984) included *Ellerkeldia rubra* (de Buen), based on Yáñez-Arancibia's (1975) report of *Scopularia rubra,* in their paper on native names of Easter Island fishes. Randall has not observed or collected *H. semicinctum* at Easter Island, despite the fact that he has collected fishes extensively there on three separate occasions, and he has not met any fishermen or divers there who are familiar with this species (J. E. Randall, pers. comm.). Consequently, Randall believes that there is no breeding population of *H. semicinctum* at Easter Island (at least not in shallow water) and that Yáñez-Arancibia's report of a specimen from Easter Island was probably of a stray or possibly of a specimen for which the locality was incorrectly recorded.

Orthography.—The correct termination for the specific name *semicinctum* is debatable. Valenciennes (1833) proposed the name in the genus *Plectropoma.* The suffix "poma" is a neuter Greek noun, whereas the suffix "cinctum" is either a neuter Latin noun or a verbal adjective, the perfect passive participle of the Latin verb "cingo." If a species-group name is a noun in apposition, it keeps the same termination without regard to the gender of the generic name with which it is associated (ICZN, Article 31b[ii]), but a species-group name that ends in a Latin participle in the nominative singular "must agree in gender with the generic name with which it is at any time combined, and its termination must be changed according to Latin inflection" (ICZN, Article 31b).

It can be argued that Valenciennes (1833) did not indicate whether he meant *semicinctum* to be a verbal adjective or a noun in apposition to *Plectropoma* because there is nothing in the original description per se to show his intent. Jordan (1891) described the genus *Gilbertia* and designated *Plectropoma semicinctum* as the type species. Further on he used the binomen *Gilbertia semicincta* and gave the etymology of *semicincta* as "semi"—half, "cinctus"—belted, indicating that he considered the second part of the compound to be a participle. The combination *Gilbertia semicincta* has been used by a number of other authors (including Boulenger 1895, Rendahl 1921, de Buen 1959, Sepúlveda Vidal & Pequeño 1985). Bauchot et al. (1984) used the binomen *Ellerkeldia semicincta*—*semicincta* agreeing in gender with *Ellerkeldia.* It appears that the evidence of usage could be considered as decisive in the sense of the Code (ICZN, Article 31b[i]), and that the specific name is a verbal adjective (spelled *semicinctus* in combination with *Hypoplectrodes*).

On the other hand it can be asserted that Valenciennes did intend *semicinctum* as a noun, because it is essentially the Latin equivalent of the last part of the French vernacular name, Le PLECTROPOME A DEMI-CEINTURES (=the plectropome with half girdles), which precedes the original description. Support for this view is given by the facts that the very next species described by Valenciennes (1833), *Mesoprion isodon,* is preceded by the French name Le MÉSOPRION A DENTS ÉGALES, that *Plectropoma nigrorubrum,* described by Cuvier (1828), is preceded by Le PLECTROPOME ROUGE ET NOIR, and that in each of these cases the specific name is a translation of the last part of the French name and the same part of speech (nouns in the first instance, adjectives in the second). We prefer this latter interpretation—that Valenciennes did indeed indicate that he regarded the name *semicinctum* as a noun, and consider the correct binomen for this species to be *Hypoplectrodes semicinctum.*

Remarks.—As mentioned in the introduction, the junior author was convinced some years ago after comparing the original descriptions that *Plectropoma semicinctum* and *Scopularia rubra* are synonymous. Because of a few discrepancies between Valenciennes' (1833) description of *P. semicinctum* and de Buen's (1959) description of *S. rubra,* the senior author disagreed. Valenciennes described the presence of three strong antrorse spines on the lower limb of the preopercle and gave the anal- and pectoral-fin ray counts as III, 7 and 15, respectively; in contrast, de Buen did not mention the presence of any preopercular spines (although he recorded the occurrence of serrae on the upper limb of the preopercle) and gave the anal- and pectoral-fin ray counts as III, 8 and 16, respectively. In de Buen's illustration of the holotype of *S. rubra* (see Fig. 5) the upper limb of the preopercle is serrate, but the lower limb is smooth. (Although de Buen mentioned *H. semicinctum,* as *Gilbertia semicincta,* in a list near the beginning of his paper, he did not compare it with *S. rubra.*)

Despite a number of attempts over a period of more than 15 years, we have been unable to find de Buen's type material of *S. rubra*; the types are apparently lost. However, we have examined the holotype of *P. semicinctum* and find that the discrepancies noted above between the two original descriptions can be easily resolved. Valenciennes' (1833) counts of III, 7 (anal-fin rays) and 15 (pectoral-fin rays) are in error. The holotype of *P. semicinctum* has an anal-fin ray count of III, 8 and pectoral-fin ray count of 16 (in each fin). (Valenciennes was also inaccurate when he recorded the dorsal-fin ray count of the holotype of *P. semicinctum* as X, 20; the correct count is X, 19. This difference is probably the result of counting the last soft ray, which is split to the base, as two elements rather than as one.) Frequently in specimens of species of *Hypoplectrodes* the antrorse spines on the ventral margin of the preopercle are covered by skin and easily overlooked, despite the fact that they are typically well developed. In view of the overall close similarity between specimens of *H. semicinctum* and de Buen's description of *S. rubra* (see Table 6), it is reasonable to assume that the preopercular spines on de Buen's specimens were obscured by skin.

In Table 6 data taken by us on specimens of *H. semicinctum* are compared with those given by de Buen on the holotype and paratype of *S. rubra*. De Buen gave total lengths, but did not give standard lengths for his material. We have estimated the standard lengths of his specimens based on our measurements of total and standard lengths of 15 specimens of *H. semicinctum* (SL = a + b [TL], where a = −5.2094, b = 0.8541, r = 0.9995). The meristic data are in close agreement; with the exception of two characters (gillrakers and scales below the lateral line) de Buen's counts fall within the ranges we obtained for *H. semicinctum*, and de Buen's counts for those two characters are just outside our ranges. De Buen's ranges for several morphometric characters fall outside our ranges. Because our morphometric data are based on a relatively small number of specimens (16 or 17), de Buen's ranges may be reasonable extensions of ours. Alternatively, in some cases de Buen's methods of measuring may have been different from ours or we may have misinterpreted his methods (see section on abbreviations and methods), perhaps as a result of not adequately translating his Spanish into English (although we had our translation edited by Dr. José Escobar, Spanish faculty, College of Charleston). In any event we consider our lack of complete agreement with de Buen's morphometric data to be relatively minor in view of the general similarity we find between de Buen's description of *S. rubra* and the specimens of *H. semicinctum* that we examined. The striking resemblance between *H. semicinctum* and de Buen's *S. rubra* can be seen by comparing Figs. 3 and 4 with Fig. 5 and by comparing the colorations of the two nominal species as described by Valenciennes and de Buen. Accordingly, then, we consider *Scopularia rubra* de Buen, 1959, to be a junior synonym of *Hypoplectrodes semicinctum* (Valenciennes, 1833). (G. R. Allen and J. E. Randall, pers. comm., have arrived at the same conclusion regarding the synonymy of *S. rubra* and *H. semicinctum.*)

Material examined.—Thirty-eight specimens, 38–177 mm SL.

Holotype: MNHN 7777 (146 mm SL); Juan Fernández Islands; C. Gay.

Other material: MCZ 4827 (two specimens, 134–141 mm SL), Juan Fernández Islands, Hassler Expd., 1872; USNM 176414 (1, 142), Cumberland Bay, Juan Fernández Islands, 33°38.0′S, 78°50′W, M. J. Lobell, 20 Feb 1945; SIO65-634 (17, 38–160), Cumberland Bay, Juan Fernández Islands, 33°38′20″S, 78°48′50″W, 6–11 m, W. Baldwin et al., 11 Dec 1965; MCZ 46165 (7, 78–177), West Bay, Más a Tierra Island, Juan Fernández Islands, 0–20 m, R/V *Anton Bruun,* cr. XIII, coll. 15, Jan 1966; CAS 24143 (4, 88–115), data as for MCZ 46165; SIO65-624 (4, 86–157), San Félix Island, NW side, 26°17′30″S, 80°05′40″W, 0–9 m,

W. Baldwin et al., 5 Dec 1965; SIO65-628 (2, 106–156), locality as for SIO65-624, 0–8 m, W. Baldwin et al., 6 Dec 1965.

Homonymy

Allen (1976) described *Ellerkeldia rubra* from Western Australia. As a result of our synonymizing *Scopularia rubra* with *Hypoplectrodes semicinctum, Ellerkeldia rubra* Allen, 1976 (=*Hypoplectrodes ruber*) becomes a junior secondary homonym of *S. rubra* de Buen, 1959. Gerald R. Allen and John E. Randall plan to propose a new name to replace *Hypoplectrodes ruber.*

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ACANTHEMBLEMARIA PAULA, A NEW DIMINUTIVE CHAENOPSID (PISCES: BLENNIOIDEI) FROM BELIZE, WITH COMMENTS ON LIFE HISTORY

G. David Johnson and Edward B. Brothers

Abstract.—*Acanthemblemaria paula* is described from the barrier reef and outlying islands of Belize. The new species is the smallest member of the Chaenopsidae, reaching sexual maturity at 11.5 mm SL or smaller and attaining a maximum size of about 18 mm SL. In addition to its small size, it differs from all other *Acanthemblemaria* by its low number of dorsal-fin spines and distinctive head spination. Confusion of *A. paula* with *A. spinosa* led previous authors to erroneous conclusions about life history parameters of *A. spinosa* and larval recruitment in *Acanthemblemaria.*

In March 1987, we made shallow rotenone collections of fishes at the north end of Carrie Bow Cay, Belize, the site of a Smithsonian Institution field station since 1972. The purpose of these collections was to obtain otoliths for analysis of daily growth increments, and, thus, all specimens were fixed in 95% ethanol. Among the fishes collected were two tiny specimens of the chaenopsid genus *Acanthemblemaria* Metzelaar that we were unable to identify using the most recent generic revision (Smith-Vaniz & Palacio 1974). The ethanol-fixed material was less than ideal for systematic study, but led us to examine the extensive holdings of Belize *Acanthemblemaria* at the Field Museum of Natural History, collected and reported on by Greenfield & Johnson (1981). There, among 12 lots identified as *A. spinosa,* we found 50 additional specimens representing what we were then able to recognize as a previously undescribed species. Returning to Carrie Bow in March 1988, we discovered that the new species is quite common on the reef flat and has habits similar to those of *A. greenfieldi.* The new species is a diminutive form, the smallest known member of the Chaenopsidae, and this may partially explain how it has gone unrecognized, despite its residence in the environs of the very active Smithsonian research facility. As currently known its geographic distribution is restricted to Belize, and specimens were not present in material examined by Smith-Vaniz & Palacio (1974). In this paper we describe the new species and discuss its bearing on the conclusions of Greenfield & Greenfield (1982) concerning life history parameters of *A. spinosa* and habitat partitioning and larval recruitment in *Acanthemblemaria.*

Methods.—Counts and measurements largely follow the methods of Stephens (1963). Pore terminology is that of Smith-Vaniz & Palacio (1974), as modified by Johnson & Greenfield (1976) and Rosenblatt & McCosker (1988). Measurements were made with an ocular micrometer. All lengths are standard length (SL) unless stated otherwise. Vertebral and median fin ray counts were made from radiographs. Tooth and gill-raker counts were determined on cleared and stained specimens. Pore counts and head spine distribution were determined from scanning electron micrographs and whole specimens. Institutional abbreviations are as follows: ANSP, Academy of Natural Sciences of Philadelphia; FMNH,

Table 1.—Frequency distributions of fin-ray and vertebral counts in three species of *Acanthemblemaria*.

	Dorsal-fin spines						Dorsal-fin soft rays								Total dorsal-fin elements						
Species	18	19	20	21	22	$\bar{x}$	13	14	15	16	17	18	19	$\bar{x}$	33	34	35	36	37	38	$\bar{x}$
spinosa[1]	—	—	24	111	11	20.9	4	71	53	13	—	—	—	14.5	1	8	67	66	9	—	35.5
spinosa[3]	—	—	2	11	1	20.9	—	10	4	—	—	—	—	14.3	—	1	9	4	—	—	35.2
aspera[1]	—	1	59	53	8	20.6	—	5	29	68	18	—	—	15.8	—	—	16	49	48	7	36.4
aspera[2]	—	3	19	1	—	19.9	—	8	14	1	—	—	—	14.7	—	9	14	—	—	—	34.6
aspera[3]	—	—	6	13	—	20.7	—	2	14	3	—	—	—	15.0	—	—	6	12	1	—	35.7
paula[3]	13	72	29	1	—	19.2	—	—	1	35	54	12	1	16.8	—	—	18	60	25	—	36.1

	Anal-fin soft rays						Pectoral-fin rays				Segmented caudal-fin rays				
Species	21	22	23	24	25	$\bar{x}$	12	13	14	$\bar{x}$	11	12	13	14	$\bar{x}$
spinosa[1]	1	10	68	67	6	23.4	10	153	3	13.0	—	—	81	—	13.0
spinosa[2]	—	3	8	3	—	23.0	—	14	—	13.0	—	—	14	—	13.0
aspera[1]	—	11	50	48	11	23.5	11	133	5	13.0	2	92	34	1	12.3
aspera[2]	5	18	—	—	—	21.8									
aspera[3]	—	3	13	3	—	23.0	—	18	1	13.0	—	11	8	—	12.4
paula[3]	—	6	60	38	3	23.4	6	60	4	13.0	4	32	36	—	12.4

	Precaudal vertebrae				Caudal vertebrae					Total vertebrae					
Species	11	12	13	$\bar{x}$	28	29	30	31	$\bar{x}$	39	40	41	42	43	$\bar{x}$
spinosa[1]	81	4		11.0	3	18	52	12	29.9	1	18	54	12		41.4
aspera[2]		54	17	12.2	2	25	35	9	29.7		2	19	30	20	42.0
paula[3]		81	7	12.1	14	59	21		29.1		13	54	27		41.1

[1] Data from Smith-Vaniz & Palacio (1974).

[2] Data from Cartagena, Colombia population (Acero 1984).

[3] Original data based on specimens from Belize.

Field Museum of Natural History; USNM, United States National Museum of Natural History.

Acanthemblemaria paula, new species

Figs. 1, 2

Acanthemblemaria spinosa (in part, not of Metzelaar, 1919) Greenfield & Johnson, 1981.—Greenfield & Greenfield, 1982.

Diagnosis.—An *Acanthemblemaria* differing from all other members of the genus by its small size (sexually mature at <12 mm, largest specimen 18.4 mm) and low number of dorsal-fin spines (18–21, $\bar{x} = 19.2$) and further distinguished by the following combination of characters: supraorbital cirrus complexly branched; head spines well developed, those on frontals extending posteriorly beyond orbits in a triangular patch reaching about two-thirds distance to dorsal-fin origin; anterior infraorbital with a few spines anteriorly, posterior infraorbital smooth.

Counts and measurements in mm of holotype.—Dorsal fin XX, 17; anal fin II, 24; pectoral fin 13. Standard length 15.9; head length 3.4; head depth 2.0; upper-jaw length 1.4; orbit length 0.6; snout length 0.5; interorbital width 0.5; predorsal length 1.9; preanal length 6.8; caudal-peduncle length 0.8; caudal-peduncle depth 0.9; orbital cirrus length 0.5; pectoral-fin length 3.3; longest dorsal-fin spine length 1.6.

Description.—Frequency distributions of fin-ray and vertebral counts are given in Table 1. Dorsal-fin spines 18–21 ($\bar{x} = 19.2$), soft rays 15–19 ($\bar{x} = 16.8$); total elements 35–37 ($\bar{x} = 36.1$). Anal fin II, 22–25 ($\bar{x} = 23.4$). Pectoral-fin rays 12–14 ($\bar{x} = 13.0$).

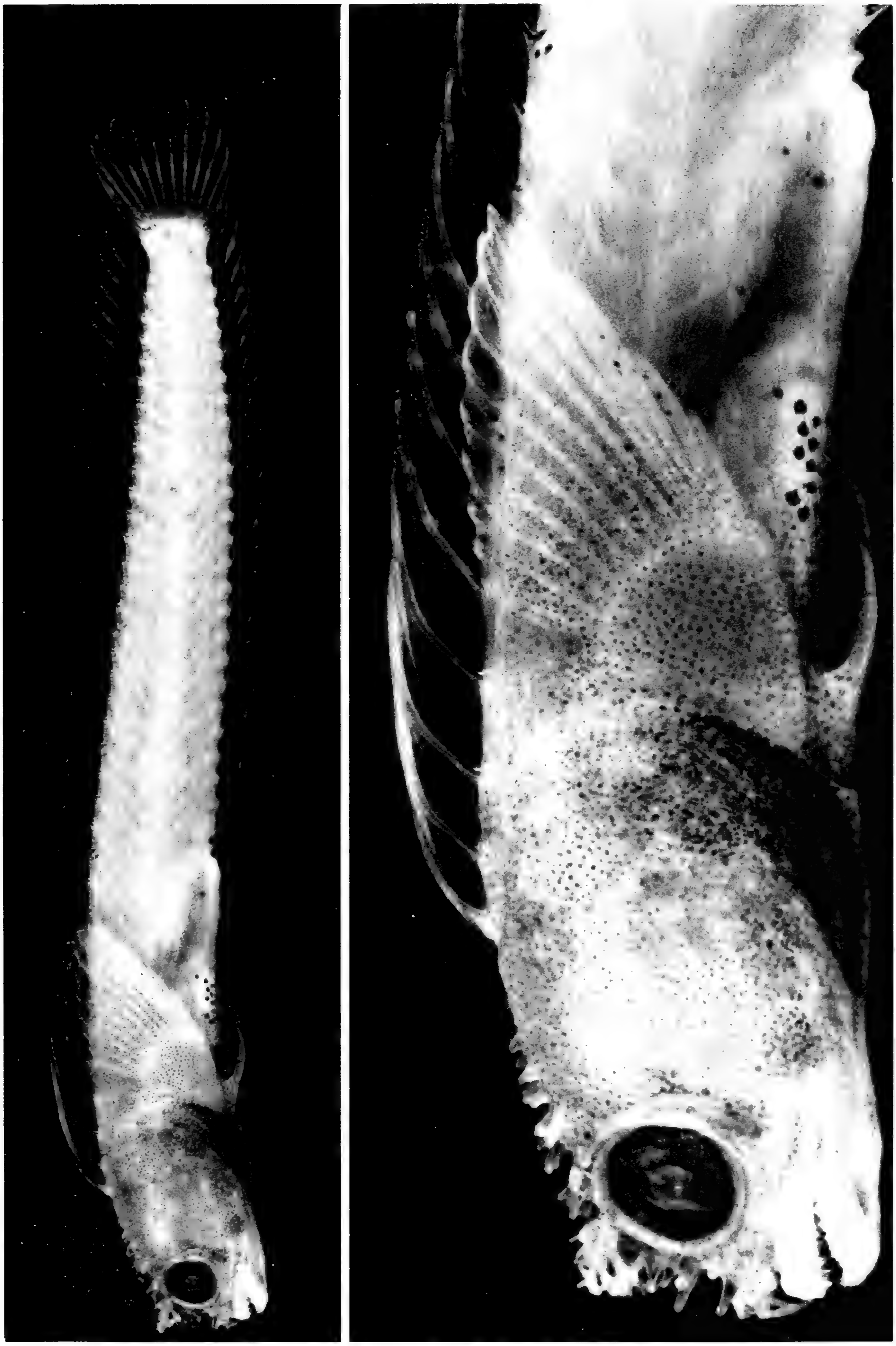

Fig. 1. *Acanthemblemaria paula*, new species, holotype, USNM 301835, male, 15.9 mm SL, Carrie Bow Cay, Belize.

Segmented caudal-fin rays 11–13 ($\bar{x} = 12.4$). Pelvic-fin rays I, 3. Vertebrae: precaudal 12–13 ($\bar{x} = 12.1$); caudal 28–30 ($\bar{x} = 29.1$); total 40–42 ($\bar{x} = 41.2$).

Body very slender and elongate, comparable to that of *Acanthemblemaria chaplini,* the most elongate and slender species of the genus; head depth 7.3–8.0 in SL (7.8 in holotype of *A. chaplini,* 5.7–7.2 in holotypes of remaining species); head length 4.5–5.0 in SL (3.0–4.4 in other species).

Cephalic sensory pores: mandibular 4; common 1; preopercular 5; posttemporal 2–3; lateral supratemporal 2–3; median supratemporal 1–2; supraorbital 1–3; posterior infraorbital 3; anterior infraorbital 3; frontal 0–1; median interorbital 1–3; anterior frontal 1.

Supraorbital cirrus complexly arborescent; main stalk usually comprising three palmate, multifid branches—a large central branch with two smaller branches arising proximally on either side of it; medial to main portion of cirrus, a smaller multifid branch arises at posterolateral margin of stalk base; cirrus generally longer in males (1–1.8 in eye) than in females (1.5–2.0 in eye). Anterior nostril on short tube, with posterior rim extended as multifid cirrus (length 1.2–2.2 in eye of males, 2.0–2.6 in eye of females).

Dorsal fin with fleshy flap on anterior margin of first spine. Membranes between adjacent spines and soft rays of dorsal fin not notably incised, continuous between tips of elements so that margin of fin is smooth; last spine slightly shorter than first soft ray, resulting in slight notch at junction of spinous and soft portions of fin. Membranes between adjacent rays of anal fin incised, extending posteriorly from tip of each ray of anterior margin of succeeding ray slightly proximal to tip, so that tip of each ray appears slightly exerted; exerted tips of all rays curved posteriorly; condition exaggerated in males wherein tissue surrounding ray tips is notably thickened. Ultimate dorsal- and anal-fin rays connected along caudal peduncle by membrane that extends to distal tips of posteriormost dorsal and ventral procurrent caudal rays. Margin of caudal fin rounded. Pectoral fin large, rounded, with weakly scalloped margin; ventralmost three rays thicker than others and with tips slightly exerted, more so in males.

Vomerine teeth 9–13, arranged in ring, frequently with one tooth in center. Each palatine with two rows of teeth, 3–7 in outer row, 1–4 in inner row (one specimen has only 3 in single row on one palatine). Each premaxilla with outer row of 8–12 teeth, flattened and pointed at tips, becoming less so posteriorly as they also decrease in size, and inner band of smaller, curved, conical teeth. Anterior expanded portion of each dentary with outer row of 7 relatively incisiform teeth, similar in configuration to outer row on premaxillae, and inner band of smaller, robust, conical teeth that continue as single row onto straight, posterior portion, where they become considerably larger. Gill rakers 3+5.

Anterior and dorsal areas of head ornamented with anteriorly directed spines (Fig. 2). Supraorbital rim of each frontal bearing row of five to six spines that extends from posterodorsal corner of orbit anteriorly to junction with lateral ethmoid and nasal where a row of spines continues on each of these bones. Each lateral ethmoid bears two spines on anterior orbital rim. Each nasal bears four spines, a vertical row of three and one lateral to the ventralmost of these. Each lacrimal bears four to five spines along anterior half of dorsolateral margin, these decreasing substantially in size posteriorly. Dorsum of cranium (frontals) with a roughly diamond-shaped patch of 17–23 spines, its anterior apex extending just anterior to a point about midway between posterior orbital rim and pupil, or slightly beyond, and its posterior apex reaching posteriorly about two-thirds distance between posterior orbital rim and dorsal-fin origin.

Color in alcohol.—Background coloration over head and body is uniformly pale cream to straw. Pigmentation is sparse and extremely variable among individuals. In addition to the intrinsic individual variability, it appears that there is substantial loss of dark pigment with time in alcohol. The FMNH specimens (all in alcohol for at least ten years) exhibit only a sparse distribution of black pigment. Fresher specimens (USNM material, preserved for about one year) exhibit the dark black melanophores that characterize the older material, but also have large numbers of fine, purplish-red pigment cells. The latter are apparently lost with long-term storage in alcohol. Due to the marked differences, FMNH and USNM specimens are described separately.

FMNH specimens: Posterior to the anus, the body surface is immaculate, although in some specimens a few internal clusters of melanophores can be detected along the vertebral column. Anterior to the anus, the amount and arrangement of external melanophores varies considerably; some individuals appear almost completely devoid of pigment, and there is no consistent pattern of melanophores and no consistent sexual dichromatism. The following description emphasizes the most consistent pigmentary features. There are frequently two sparse clusters of internal melanophores in the ventrolateral area of the abdominal cavity just anterior to the anus; melanophores also may be scattered variously along the mid-ventral and ventrolateral surfaces of the anterior portion of the abdominal cavity, in the area below the pectoral fin. The abdominal pigmentation frequently consists of two posterodorsally directed crescents, one just anterior to the anus and the other just ventral to the pectoral fin. Small individual melanophores occasionally occur on the dorsal half of the body surface, usually anterior to a vertical from the anus. Branchiostegal rays and membranes may be unpigmented, or covered with scattered or densely packed melanophores; ventrally, the anterior rays are more heavily pigmented, but in some specimens melanophores also occur at the dorsal tips of the most posterior rays, where they curve anteriorly above the opercle. In occasional specimens, there are a few melanophores on the cheek just anterior to the angle of the preopercle. The iris is uniformly black, otherwise the head lacks pigment. The pectoral fin may be immaculate, have a sparse sprinkling of melanophores, or have a more regular arrangement of melanophores along the dorsal and ventral edges of many of the rays, the latter usually being denser on the medial side of the fin; in a few specimens the ventral portion of the pectoral-fin base is pigmented. The pelvic-fin base and rays range from immaculate to relatively heavily pigmented. Frequently there are several sparse clusters of melanophores irregularly placed along the spinous dorsal fin, more or less associated with the more distal portions of individual spines; these sparse clusters begin posterior to the fifth spine, but in occasional specimens there is a larger, denser concentration of pigment on the membrane between the third and fourth spines. Dorsal soft rays are more consistently pigmented, most specimens having many rays with several mostly dash-like melanophores lying along their anterior and/or posterior edges. Similar pigment occurs much less frequently on the anal-fin rays. Most caudal-fin rays have dash-like melanophores along their dorsal and ventral edges.

USNM specimens: The melanophore patterns described above also characterize the fresher USNM specimens and will not be repeated here, where we describe only the additional purple-red pigment cells, referred to, for convenience, as "P-phores." Both the persistent black melanophores and the transient P-phores are evident in the black-and-white photograph of the holotype (Fig. 1), where the dichotomy is evidenced to some extent in relative intensity of the spots. In fresh, unpreserved specimens, there is no detectible dichotomy, that is, all dark pigment cells appear black. Soon after formalin fixation, the majority of these dark spots fade to purplish-red and, with long-term storage in alcohol, apparently

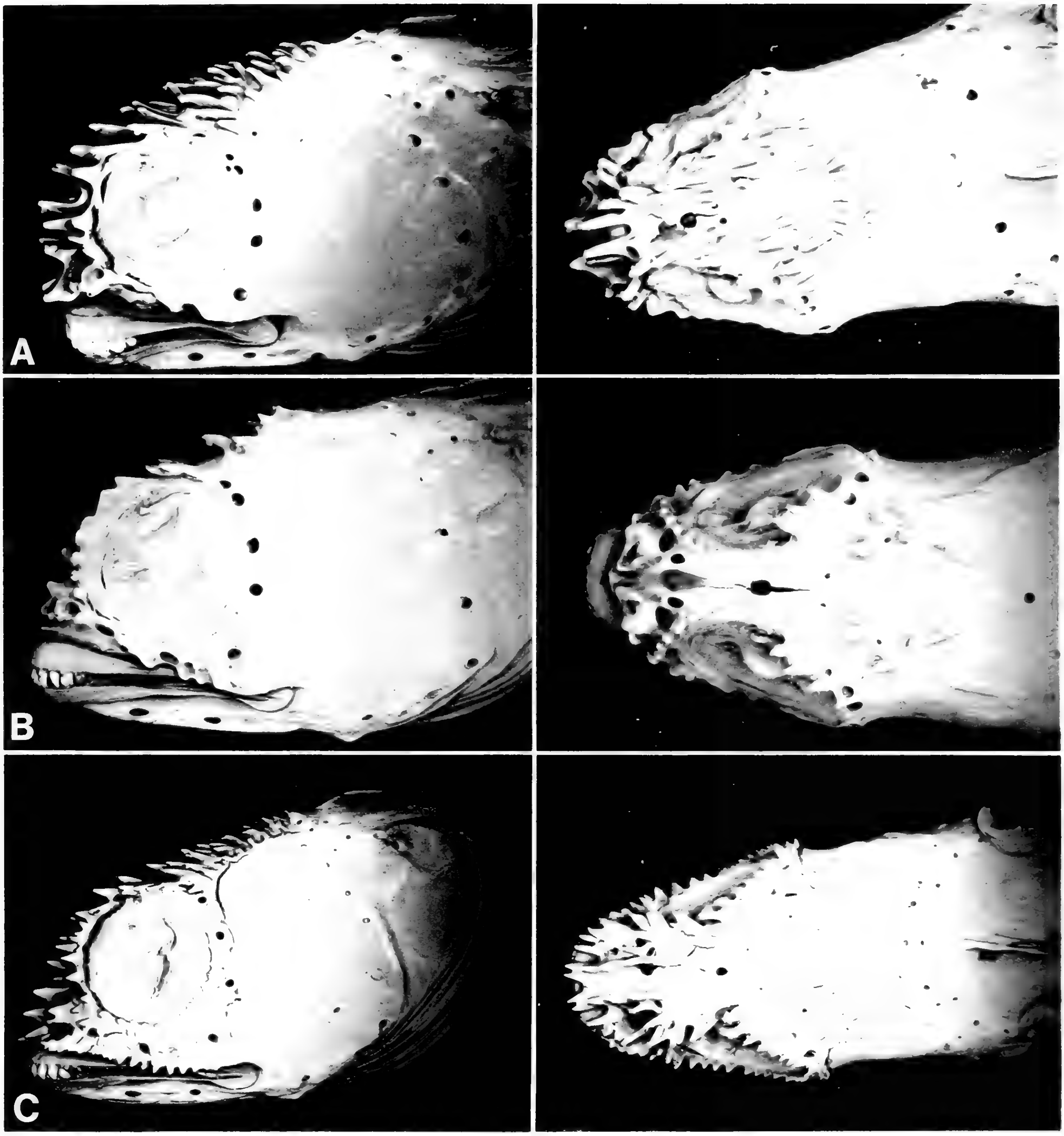

Fig. 2. Scanning electron micrographs illustrating head spines and cephalic sensory pores of three species of *Acanthemblemaria* in lateral (left) and dorsal (right) views; all males, supraorbital cirri removed. (A) *A. paula,* FMNH 90876, 15.4 mm SL; (B) *A. aspera,* USNM 276052, 19.1 mm SL; (C) *A. spinosa,* USNM 198276, 21.6 mm SL.

continue fading, eventually disappearing to leave only the black melanophores described above. (In rare specimens some pigment cells with distributions characteristic of P-phores appear black.) In all specimens, a fine speckling of P-phores begins in the pectoral region of the body at about the level of the sixth to eighth dorsal spine and extends anteriorly to cover much of the head, including the opercular series, branchiostegal membranes, pectoral-fin base and about half the surface of the fin, pelvic-fin base and rays and, in some specimens, the membrane between the first four or five dorsal spines. The densest concentration of P-phores is seen on the branchiostegal membranes of some males; females tend to have this area more lightly pigmented, but this sexual difference is inconsistent. On the head, the most sparsely pigmented areas are the cheek, anterior portion of the cranium, and the jaws, which are frequently immaculate; denser concentrations are found just posterior and ventral to the orbit, forming one or two oblique bars. Superficial and subcutaneous P-phores may also be apparent on the abdomen, where they may be associated with the two distinctive crescents described for the melanophores. Dorsal to these, one or two small clusters of superficial P-phores occur on the upper body in some specimens. Deep, internal blocks of P-phores may be present on six to eight centra along the length of the body, and, in such specimens, there are usually clusters of P-phores at the bases of every second or third dorsal- and anal-fin ray. These clusters begin internally around the pterygiophores and may rise to the surface at the fin-ray bases, sometimes extending a short distance along the rays. P-phores are also found along the bases of some caudal-fin rays.

In USNM specimens that were retained in formalin for several months before transfer to ethanol, white pigmentation (leucophores) is evident in discrete patches on the head, fins, and body. There is a prominent white patch or oblique bar, bordered by the two purple-red bars, on the lower portion of the cheek immediately posterior to the orbit. There is a triangular white patch on the dorsum of the cranium between and immediately posterior to the orbits, the iris is white with a speckling of P-phores, and the supraorbital cirrus is white. Several discrete white patches occur on the opercular series and branchiostegal membranes, and the entire gular region is white. Leucophores are also prominent on the pelvic-fin rays and the pectoral-fin base and proximal one-third or more of the fin. Large areas of white pigment may be seen internally on the abdomen, and smaller superficial clusters may be seen on the body dorsal to this. The membrane between the first four to seven dorsal spines is white. Internal and superficial leucophores at the bases of dorsal- and anal-fin rays alternate with the similarly placed P-phores described above.

Live color.—The following description is based on specimens that were placed on ice while still alive, painted with full strength formalin to fix the fins, and photographed immediately thereafter. All pigment described above is evident, but, as noted, melanophores and P-phores are indistinguishable. The head and anterior body (to about the anus), including the pelvic and proximal portion of the pectoral fins, appear predominantly white with prominent black and greenish-yellow (xanthophores) markings. Two distinctive black crescents are evident on the silvery-white background of the abdomen. Xanthophores are in close association with melanophores (and P-phores), so that their distribution is essentially completely overlapping. The large white blotch covering the anterior portion of the spinous dorsal fin is a very prominent feature. Posterior to the anus, the body is transparent with alternating white and dark markings along the lateral midline and median fin bases. Most distinctive is a series of seven to eight rectangular blocks of white pigment lying internally along the vertebral column, each encompassing two to four centra. These white blocks are bordered on either side by narrower, less circumscribed, dark greenish marks that frequently extend to the bases of the dorsal and anal fins.

Sex.—Specimens are easily sexed based on genital morphology. Males have a single papilla at the posterior margin of the anus, whereas in females the anus is surrounded by a papillar fringe. The ratio of males to females in both the USNM and FMNH collections is about two to one. Because most specimens were collected individually with quinaldine, we cannot discount the possibility that the sex ratio is partially a reflection of collecting bias. Nonetheless it seems likely that males significantly outnumber females in the natural population. Greenfield & Greenfield (1982) reported that males of *Acanthemblemaria spinosa* and *A. greenfieldi* significantly outnumbered females in their collections, and Rosenblatt & Stephens (1978) reported that sex ratios in their collections of *Mccoskerichthys sandae* was strongly biased in favor of males.

There appears to be no pronounced sexual dimorphism; however, as described above, males tend to have slightly larger supraorbital and nasal cirri and usually have the tips of the anal-fin rays notably thickened and more strongly curved. Males also tend to have more intense and extensive dark pigmentation on the branchiostegal membranes than do females, but this is not a consistent difference. Males ranged in length from 10.1 mm to 18.4 mm with a mean of 14.8 mm, whereas females ranged from 10.3 mm to 16.7 mm with a mean of 13.1 mm. Size at sexual maturity and fecundity are discussed below.

Etymology.—*Paula,* Latin for little, in reference to the diminutive size of this fish, the smallest member of the Chaenopsidae, here used as a noun in apposition. The name was chosen to honor Paula Keener, who participated in the collection that resulted in recognition of this species.

Habitat.—*A. paula* occupies burrows made by invertebrates (usually those of sipunculids) in dead coral in shallow water (<5 m) on both sides of reef crest and on pavement zone of reef flat.

Distribution.—Known only from the barrier reef and outlying atolls of Belize.

Material examined.—114 specimens (10.1–18.4 mm) in 20 collections, all from Belize.

Holotype.—USNM 301835, 15.9 mm male taken with quinaldine from dead coral on reef flat at south end of Carrie Bow Cay, Belize, at depth of 1–2 m on 22 Mar 1988, by G. D. Johnson, and party.

Paratypes.—Carrie Bow Cay. South end of island, depth 1.0–2.5 m, coral rubble and pavement zone on reef flat: FMNH 90876 (17, 13.8–18.4, 3 prepared for SEM), 4 Jan 1978, D. W. and T. A. Greenfield, and C. Rakocinski; FMNH 90869 (8, 12.9–16.6), 17 May 1977, D. W. and T. A. Greenfield; USNM 301831 (3, 13.1–16.7), 21 Mar 1988, G. D. Johnson; USNM 301836 (4, 13.4–15.1), 22 Mar 1988, E. B. Brothers, R. A. Fritzsche, and G. D. Johnson; USNM 301832 (10, 11.6–17.0), 25 Mar 1988, G. D. Johnson; ANSP 162806 (6, 11.8–16.0), 26 Mar 1988, G. D. Johnson; USNM 301833 (23, 12.1–16.7), 28 Mar 1988, R. A. Fritzsche and G. D. Johnson; SIO 89-14 (1, 15.4), 19 Nov 1988, R. A. Fritzsche; SIO 89-13 (5, 11.6–15.3), 19 Mar 1989. North end of island, coral and coral rubble just outside reef crest, 2–5 m: USNM 290669 (2, 12.4–14.9), 24 Mar 1987, E. B. Brothers, G. D. Johnson, and P. Keener; USNM 301834 (9, 10.3–15.2, cleared and stained), 17 Mar 1988, E. B. Brothers, R. A. Fritzsche, G. D. Johnson, and P. Keener. East side of island, just inside reef crest, 1–2 m: FMNH 98298 (3, 13.9–15.0), 16 May 1977, D. W. and T. A. Greenfield; USNM 301830 (3, 10.8–14.7), 27 Mar 1988, E. B. Brothers, R. A. Fritzsche, and G. D. Johnson. Collection site unspecified: FMNH 89372 (1, 14.8), 2 Jan 1978, D. W. Greenfield et al.; FMNH 89328 (2, 15.2–15.8), 14 May 1977, D. W. Greenfield.

Glover's Reef. Cay in shallow water behind cabin no. 9: FMNH 90497 (12, 12.0–15.5), 14 Jun 1978, G. Glodek, D. W. Greenfield, and R. K. Johnson. West side of Long Cay, about 200 yards south of cabin no. 9: FMNH 98296 (1, 14.2), 9 Jun 1978, G. Glodek and T. Murphy. Collection site unspecified: FMNH 77558 (1, 13.5), 29 Jul 1973, D. W. and T. A. Greenfield.

Buttonwood Cay. One mile south of island: FMNH 86085 (3, 11.7–13.6), 23 Jul 1974; FMNH 86088 (1, 10.1), 23 Jul 1974.

Sargeant's Cay. FMNH 98297 (2, 11.6–12.4).

Ambergris Cay. 2.5 miles north of San Pedro: FMNH 98295 (1, 14.8).

Discussion.—A cladistic analysis of relationships within *Acanthemblemaria* is beyond the scope of this study. Furthermore, although Stephens' (1963) surmise that *Ekemblemaria* is the closest relative of *Acanthemblemaria* seems reasonable, character polarity for *Acanthemblemaria* remains problematic in the absence of a well-corroborated cladistic hypothesis of generic relationships for the Chaenopsidae. Based on unpolarized similarities, we believe that *A. paula* is probably most closely related to *A. aspera* and *medusa,* two species that Smith-Vaniz & Palacio (1974) hypothesized to be closely related, but this remains to be tested cladistically. These three species (*paula, aspera* and *medusa*) share complex, deeply branched supraorbital cirri not found in other members of the genus. Head spines in *A. paula* are long as in *A. maria* and *spinosa* but not as numerous. Distribution of spines on top of the head is more like that in *A. aspera* and *medusa,* wherein there is a triangular patch on the frontals extending posteriorly from the orbits. In *paula* this area is completely covered with spines, whereas in *aspera* and *medusa* it is largely smooth (Fig. 2). The extreme development of fleshy papillae that uniquely characterizes *A. medusa* is lacking in *paula,* and several characters suggest that *paula* and *aspera* are most closely related. They share the lowest dorsal-fin spine count in the genus ($\bar{x}$ = 19.2 and 20.5, respectively; 21.7 in *medusa*) and the lowest segmented caudal-fin ray count among Atlantic species ($\bar{x}$ = 12.4 and 12.3; 13.0 in *medusa*; data not available for eastern Pacific species). Finally, the color patterns of *A. paula* and *aspera* resemble one another more closely than they do that of any other species. Preserved specimens lack any regular external pigment pattern consisting of repeated bars, stripes or spots.

Acanthemblemaria paula may mature at sizes smaller than any known blennioid, although data in size at sexual maturity is lacking for most species. Females of *A. paula* may be ripe at 11.5 mm and individuals smaller than 11.0 mm may have developing eggs. Among the smallest known blennioids are the blenniid, *Medusablennius chani* (Springer, 1966) and the labrisomid, *Starksia nannodes. Medusablennius chani* is known from ten specimens ranging in size from a 12.1 mm ripe female to a 15.4 mm immature male (Smith-Vaniz & Springer 1971). Specimens of *S. nannodes* examined by Bohlke & Springer (1961) ranged from 10.5 to 17.0 mm with a 13.1 mm ripe female. There is little published information on size at sexual maturity in chaenopsids, but all species attain maximum sizes larger than *A. paula* (18.4 mm). Within *Acanthemblemaria,* specimens 30 mm or longer (some >50 mm) are known for all 15 species. Whatever the precise relationships of *A. paula* to other species of the genus, its small size is unquestionably derived.

Weitzman & Vari (1988) listed 85 species representing five orders and 11 families of miniature Neotropical freshwater fishes. Miniature species were considered by Weitzman and Vari to be those that either are known to mature sexually at less than 20 mm and may reach slightly larger sizes (<25–26 mm), or for which maturity data are unknown but which are not reported to exceed 25–26 mm in the wild. By those criteria, *Acanthemblemaria paula* is unequivocally a miniature species. The elongate body and relatively small head further emphasize its miniature stature; wet weights of 15 specimens, 13.4–16.4 mm in length, ranged from a mere 15 to 25 mg.

Weitzman & Vari (1988) noted that all species in their list of miniatures that had been examined in detail exhibit numerous apparently paedomorphic morphological reductions, particularly in the degree of development of the laterosensory canal system of the head and body, sculpturing on the bones of the head and total numbers of fin rays and body scales. The state of these and other characters in *A. paula* indicates that miniaturization does not always involve obvious reductive paedomorphic expression. The laterosensory ossifications and pores (Fig. 2) of *A. paula* appear no less developed than in other species of the genus. Head spination is among the most extensive in the genus and considerably more pronounced than that of *A. aspera,* the putative closest relative, which reaches a maximum size of about 35 mm. Total numbers of dorsal- and anal-fin rays are lower than those of some species but higher than others and not reduced compared to those of *aspera.* Stephens (1963) also noted the lack of correlation between reduced body size and numbers of dorsal- and anal-fin rays among other species of *Acanthemblemaria.* Pectoral-fin ray counts do not differ substantially among species of *Acanthemblemaria,* and all chaenopsids lack scales, so no intrageneric comparisons of states of these characters can be made. We have identified only two features (neither absolute reductions) of *A. paula* that might be interpreted as paedomorphic. Although the total number of dorsal-fin elements is equal to that of *aspera, paula* has one more soft ray and one fewer spine; in fact, the mean dorsal-fin spine number (19.2) is the lowest in the genus. If transformation of the posteriormost dorsal-fin spines from soft rays occurs ontogenetically in chaenopsids, as it does in many percomorphs, the dorsal-fin ray composition of *A. paula* could be interpreted as paedomorphic with respect to the other species. The very slender, elongate body of *A. paula,* equalled in only one other species, *A. chaplini,* could also be seen as paedomorphic, because chaenopsid larvae are relatively more elongate than adults. It seems clear that the marked reductive features that characterize miniaturization in Neotropical freshwater fishes and at least some marine fishes (e.g., some gobioids, Springer 1983, 1988), are not universally associated with extreme size reduction.

In a study of habitat and resource partitioning between *Acanthemblemaria spinosa* and *A. greenfieldi,* Greenfield & Greenfield (1982) compared ecological and life history parameters of the two species. All subsequent references herein to G&G pertain to that paper. They found that *A. spinosa* occurs only on horizontal surfaces of dead coral whereas *A. greenfieldi* occurs only on vertical surfaces, but they noted an apparent exception in their collections. One collection made in a typical *A. greenfieldi* habitat (coral rubble and pavement zone of the back reef) contained, in addition to 36 specimens of *A. greenfieldi,* 17 specimens identified as "young *A. spinosa.*" Catalog numbers were not given, but based on the date, locality and number of specimens, we conclude that that collection is FMNH 90869, which consists of 17 specimens of *A. paula.*

A total of 90 specimens identified as *A. spinosa,* collected at Carrie Bow Cay 10–17 May 1977 and 1–4 Jan 1978, were analyzed by G&G for length frequency, stomach contents and fecundity. Of these, 30 are actually *A. paula.* Consequently, most of G&G's conclusions about life history parameters of *A. spinosa* are invalid. We did not attempt to reanalyze their data, because all 90 specimens were not used in determining each parameter and we were unable to determine how many *A. paula* were included in each analysis. Most profoundly affected are the data on size at sexual maturity and fecundity. Their observation that *A. spinosa* females mature as small as 12.4 mm is clearly based on specimens of *A. paula.* We examined 25 female *A. spinosa,* ranging in size from 11.6 to 20.4 mm; the smallest ripe individual was 15.6 mm and the mean size of ripe individuals was 18.4 mm. Of 22 female *A. paula,* 10.3–16.7 mm, the smallest ripe specimen was 11.5 mm, and the mean size of ripe specimens was 13.6 mm.

Conclusions regarding average brood size in *A. spinosa* were also affected by inclusion of several specimens of *A. paula.* Based on data presented in fig. 218 of G&G, the number of eggs per brood in *A. spinosa* ranged from 5 to 25 with a mean of 12.8. If specimens smaller than 15 mm (presumably all *A. paula*) are removed from the data, brood size ranges from 8 to 25, with a mean of

14.8. This probably still includes some specimens of *A. paula,* in which the brood size is substantially smaller, but is in better agreement with our own data from ten specimens of *A. spinosa* with a range of 9 to 30 and a mean of 17.2. Among sixteen specimens of *A. paula,* numbers of eggs per brood ranged from 1 to 10, with a mean of only 4.7. This conforms with our single observation of eggs in a burrow of a male *A. paula*; the clutch consisted of only four eggs, all apparently close to hatching. The egg size of *A. paula* and *spinosa* is roughly the same with the largest eggs averaging 0.7–0.8 mm in diameter.

Misidentification of *A. paula* led G&G to the following speculation about larval recruitment in *Acanthemblemaria*:

> The 4 January 1978 collection from a typical *Acanthemblemaria greenfieldi* habitat, which also yielded young of *A. spinosa,* provides valuable information concerning the interactions of these two species. Although the adults exhibit complete habitat separation, apparently planktonic larval *Acanthemblemaria* species settle and occupy any available hole or crevice. Because individuals of *A. spinosa* found here were only 18.4 mm or less, it may be assumed that when they outgrow their holes and search for a larger hole, they are excluded by *A. greenfieldi* from this habitat.

Because the young *A. spinosa* referred to above are actually adult *A. paula,* these conclusions are unsubstantiated. There is no evidence that individuals of *A. spinosa* occupy the specific *A. greenfieldi* habitat at any stage of their lives. In contrast, individuals of *A. paula* occupy this habitat throughout their lives and are not excluded by *A. greenfieldi* as they grow; in fact, the specific collection referred to by G&G contains the two largest known specimens of *A. paula.* Coexistence is undoubtedly facilitated by the fact that the diminutive *A. paula* utilizes small burrows that are unavailable to the much larger adult *A. greenfieldi*; according to G&G, *A. greenfieldi* matures at 19.0 mm (almost twice the size for *A. paula*) and reaches a maximum size of 32.5 mm with mean sizes of 25.5 and 23.5 for males and females, respectively. Thus, although adults of *A. paula* may compete for space with newly settled or juvenile *A. greenfieldi,* there is fine-grain habitat (refuge) partitioning between adults of the two species. This would be worth further investigation with respect to the findings of Stephens et al. (1970) on *Hypsoblennius jenkinsi.* Those authors found that maximum size of individuals was controlled by size of available tubes and hypothesized that individuals that outgrew the available tubes were subject to a greater risk of predation.

Our observations at Carrie Bow Cay on the microhabitat distribution of *A. paula* and *greenfieldi* failed to establish a clear-cut specificity to either vertical or horizontal surfaces; in areas where both surfaces were abundant, both were occupied. In a single collection (19 Mar 1989) using quinaldine just inside the reef crest we took: 7 specimens of *greenfieldi* and 8 of *paula* from vertical surfaces; 6 of *greenfieldi* and 13 of *paula* from oblique surfaces; and 2 of *greenfieldi* and 8 of *paula* from horizontal surfaces. We found these two species limited to horizontal surfaces only far back on the reef flat, where vertical surfaces are much less prevalent. *Acanthemblemaria spinosa* does not occur far inside the reef crest and appears to live primarily on vertical surfaces. Discussion by G&G of competitive interaction and displacement among *Acanthemblemaria* species is speculative and not supported by evidence that shelter is a resource limiting population size. Hastings (1984) demonstrated the latter for *A. crockeri,* and similar experimental field manipulations of the habitat and/or fishes will be necessary to elucidate the nature of interspecific interactions between the species in question here. G&G made a valuable contribution by emphasizing and reviewing the potential significance of very subtle differences in habitat utilization in small, cryptic reef fishes.

Fish community ecologists have shown an understandable bias for larger and more conspicuous fishes such as wrasses, damselfishes, surgeonfishes, butterflyfishes, etc. Population and behavioral characteristics of such groups may be entirely different from those of the diminutive, cryptic and frequently speciose blennies, gobies, eels, ophidioids, dactyloscopids, etc. Although some work has been done on chaenopsids and other blennies (e.g., Lindquist 1985, Stephens et al. 1966, Wirtz 1983), we remain largely ignorant of the demography, life history and recruitment biology of such fishes.

The very small size of *Acanthemblemaria paula* and some of its congeners raises a number of interesting questions, particularly with respect to longevity, fecundity and larval ecology. How can such species maintain populations when females apparently produce so few eggs in a lifetime? *Acanthemblemaria* species lay demersal eggs that presumably hatch to a planktonic larval stage. Based on otolith microstructure (Brothers et al. 1983) we have made preliminary determinations of the planktonic duration of the larvae of four species in the genus (*paula, aspera, greenfieldi, spinosa*). All show stereotypic "settlement marks" at presumptive ages of 22 to 25 days. A larval period of this magnitude is equal to or longer than that exhibited by many larger reef species having instantaneous fecundities hundreds to many thousands of times greater (e.g., Brothers & Thresher 1986). Do these chaenopsid blennies have any special ecological and/or behavioral adaptations that reduce larval mortality in the plankton? Do they bypass the planktonic phase completely? Detailed life history studies of small, short-lived reef species will undoubtedly yield many surprises.

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A NEW SPECIES OF *EUPSOPHUS* (ANURA: LEPTODACTYLIDAE) FROM CONTULMO, NAHUELBUTA RANGE, SOUTHERN CHILE

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Abstract.—*Eupsophus contulmoensis,* a new species of leptodactylid frog is named from the locality of Contulmo, Nahuelbuta Range, Southern Chile. This species is distinguished from its congeners by the dark-purple dorsum and the bright yellow coloration of its belly. This frog displays lumbar amplexus and is known only from the type locality.

The Nahuelbuta Range is that part of the Chilean Coastal Range bounded to the northeast by the Biobio river and to the south by the Imperial river (see Fig. 1). This mountainous area of southern Chile is approximately 175 km in length and reaches 1530 m at its greatest elevations (Alto de Nahuelbuta). The Nahuelbuta Range is covered by *Nothofagus* temperate forest and at elevations of more than 1000 m the conifer *Araucaria araucana* is present.

In this area three endemic anuran species are found (*Telmatobufo bullocki, Alsodes vanzolinii,* and *Alsodes barrioi*) (Schmidt 1952, Formas 1981, Veloso et al. 1981). Nonendemic species include: *Bufo rubropunctatus, Pleurodema thaul, Rhinoderma darwinii, R. rufum, Hylorina sylvatica, Batrachyla leptopus, B. taeniata, Eupsophus roseus,* and *E. vittatus.*

The Nahuelbuta Range shows a high degree of human-induced disturbance (pine groves of *Pinus radiata*) and little original forest remains. One of these areas is the Natural Monument of Contulmo (37°02′S; 78°12′W), where a series of herpetological collections were made between 1986 and 1987. As a result of this fieldwork a new species of frog of the genus *Eupsophus* was collected.

Eupsophus contulmoensis, new species
Fig. 2

Holotype.—MZUC (Museo de Zoología, Universidad de Concepción, Chile) 17141, adult female collected by Hector Ibarra-Vidal, 10 Jul 1987 at Contulmo, Malleco Province, Nahuelbuta Range, alt. 700 m, 15 km W (by road) of Purén, Chile (Fig. 1).

Paratypes.—Four adults (MZUC 17142, 17145, 17148, 17149) and one subadult (MZUC 17144) collected at the type locality.

Diagnosis.—A medium-sized species of *Eupsophus* (34.0–42.5 mm SVL), distinguished from its congeners (*E. roseus, E. migueli, E. calcaratus, E. insularis* and *E. vittatus*) by the dark purple dorsal pigmentation and bright yellow belly; upper part of the iris bronze-yellow in life and inner palmar tubercle prominent.

Description of adult (based on five fixed specimens).—Head slightly wider than long. Snout rounded in dorsal and lateral view, canthus rostralis concave, loreal area slightly concave, nostrils located laterally, at middistance between snout tip and orbit; eye length greater than distance between eye and nostril; interorbital distance smaller than eye length but greater than internarial

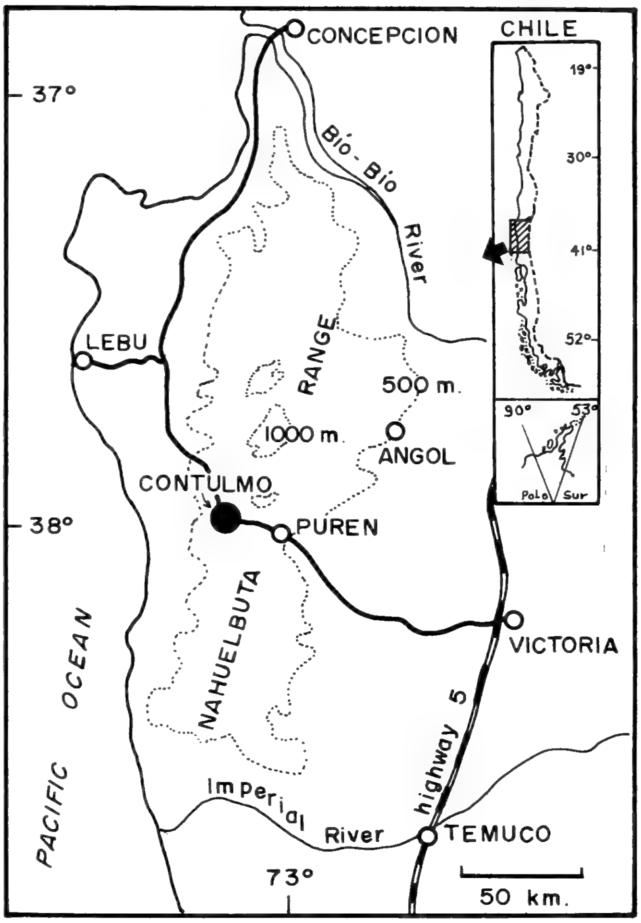

Fig. 1. Situation of the type locality (Contulmo) of *E. contulmoensis.*

distance. Tympanic membranes present and well developed. Supratympanic fold absent. Tongue round, notched at tip. Choanae rounded, dentigerous processes of vomers lying below the choanae; each process bearing five or six sharp teeth.

Forelimbs slender, first finger equal in length to second, third finger much longer than fourth; digital length in decreasing order 3-4-2-1. Palmar webbing absent; tips of fingers rounded and slightly protuberant. Inner palmar tubercle prominent; outer palmar tubercle ovoid and well developed; subarticular tubercles rounded and moderate in size; supernumerary palmar tubercles absent. Toes long, slender; tips of toes round; third and fifth equal in length; toes in decreasing order of length 4-(3,5)-2-1. Inner metatarsal tubercle ovoid and prominent; supernumerary tubercles absent; outer metatarsal tubercle tiny. Rudiment of web between toes.

Fig. 2. *Eupsophus contulmoensis,* new species. Holotype (MZUC 17141), female.

Anal opening rounded and directed postero-ventrally at dorsal level of thighs.

Dorsal and ventral skin smooth. Two faintly marked folds extending from posterior part of eye to the midlateral part of body.

Pectoral girdle arciferal; omosternum cartilaginous with short thin stem; tip sharply acute; sternum rectangular in shape with slight median constriction, its tip rounded and almost completely calcified. External measurements are shown in Table 1.

Color and color patterns.—In life dorsal ground color of head and body dark purple, two specimens (MZUC 17142, 17148) with yellow vertebral line (Fig. 3); dorsal limb surfaces dark purple with small yellow irregular spots; throat dark brown with minute irregular yellow spots; ventral surface brown and marbled with yellow; two specimens (MZUC 17141, 17144) with immaculate bright yellow abdomen; ventral surface of limbs with yellow irregular spots; yellowish irregular marks on side of head and body; upper part of iris bronze-yellow.

In alcohol dorsal surfaces dark brown and

Table 1.—Measurements of the type series of *Eupsophus contulmoensis* (mm).

	Holotype MZUC 17141 female	MZUC 17142 female	MZUC 17145 female	MZUC 17148 female	MZUC 17149 male	MZUC 17144 male subadult
Snout–vent length	45.2	39.4	43.0	44.4	38.1	34.0
Tibia length	24.2	24.5	23.5	23.4	21.4	19.5
Foot length	34.1	33.3	30.8	33.8	31.6	26.5
Head length	15.3	13.8	13.9	14.8	15.4	11.9
Head width	16.3	16.2	16.2	17.2	15.7	12.7
Interorbital distance	5.5	4.5	4.7	5.1	5.5	3.7
Internarial distance	3.7	3.7	4.3	4.3	4.1	3.3
Diameter of eye	6.1	5.2	5.1	5.4	5.6	4.1
Diameter of tympanum	2.6	2.6	2.2	2.7	2.1	1.6
Eye–nostril	4.4	4.1	2.9	3.4	2.7	2.3

vertebral line whitish; ventral areas brown and whitish spotted.

Distribution.—Known from the type locality.

Etymology.—The specific name of this frog is after the type locality.

Natural history.—The type locality, Contulmo, is a small natural reserve (approximately 1 km^2), in the Nahuelbuta Range, where the original *Nothofagus* forest yet survives. Contulmo is situated in the mediterranean perhumid region (di Castri 1968). The annual mean temperature is 12.6°, the relative humidity is 82% and the annual mean rainfall is 1896 mm (Hajek and di Castri 1975). The following trees occur there: *Nothofagus oblicua, N. dombeyi* (Fagaceae), *Eucryphia cordifolia* (Eucryphiaceae), *Persea lingue* (Lauraceae), *Laurelia phillipiana* (Monomiaceae), and *Aetoxicum punctatum* (Aetoxicaceae). The climber *Lapageria rosea* (Phileseaceae) was observed on logs. Ferns (*Lophosoria quadripinnata,* and *Ctenitis spectabilis*) and the moss *Dendroligotrichum dendroides* were collected on the ground. During winter, frogs were collected under decaying logs and stones near streams.

The following species of amphibians were also collected at the type locality: *Eupsophus roseus, E. vittatus, Batrachyla leptopus,* and *Rhinoderma darwinii.*

A female collected in spring (Nov 1987) had 65 white oocytes (1.14–2.28 mm diameter) in its ovaries, and a male had testes 4.6 mm in length. Mature males did not have nuptial asperities in winter, however the gular areas were darker than in the animals collected. In the laboratory inguinal amplexus was observed.

The stomach contents of two *Eupsophus contulmoensis* collected on 7 Nov 1987, were examined. Both specimens were killed just after capture. The following food items were identified: Oligochaeta (4), Aranea (3), Diplopoda (2), Coleoptera (2), Diptera (1), Collembola (1), and Formicidae (1). Two specimens collected in 5 Sep 1987 had empty stomachs.

Comparisons

Eupsophus contulmoensis is a frog of moderate size ($\bar{x}$ = 42.0 mm snout–vent length) as are *E. calcaratus* ($\bar{x}$ = 35.1 mm, Formas & Vera 1982), *E. migueli* ($\bar{x}$ = 35.5 mm, Formas 1978), *E. roseus* ($\bar{x}$ = 36.0 mm; Cei 1962), and *E. insularis* ($\bar{x}$ = 39.3 mm, Formas & Vera 1982). These species are notably smaller than *E. vittatus* ($\bar{x}$ = 59.4, mm Grandison 1961). *Eupsophus contulmoensis* and *E. insularis* differ in the dorsal color and in the shape of the tip of the sternum. The latter species is dark brown with yellow irregular spots on the dorsum and the sternum is truncated whereas *E.*

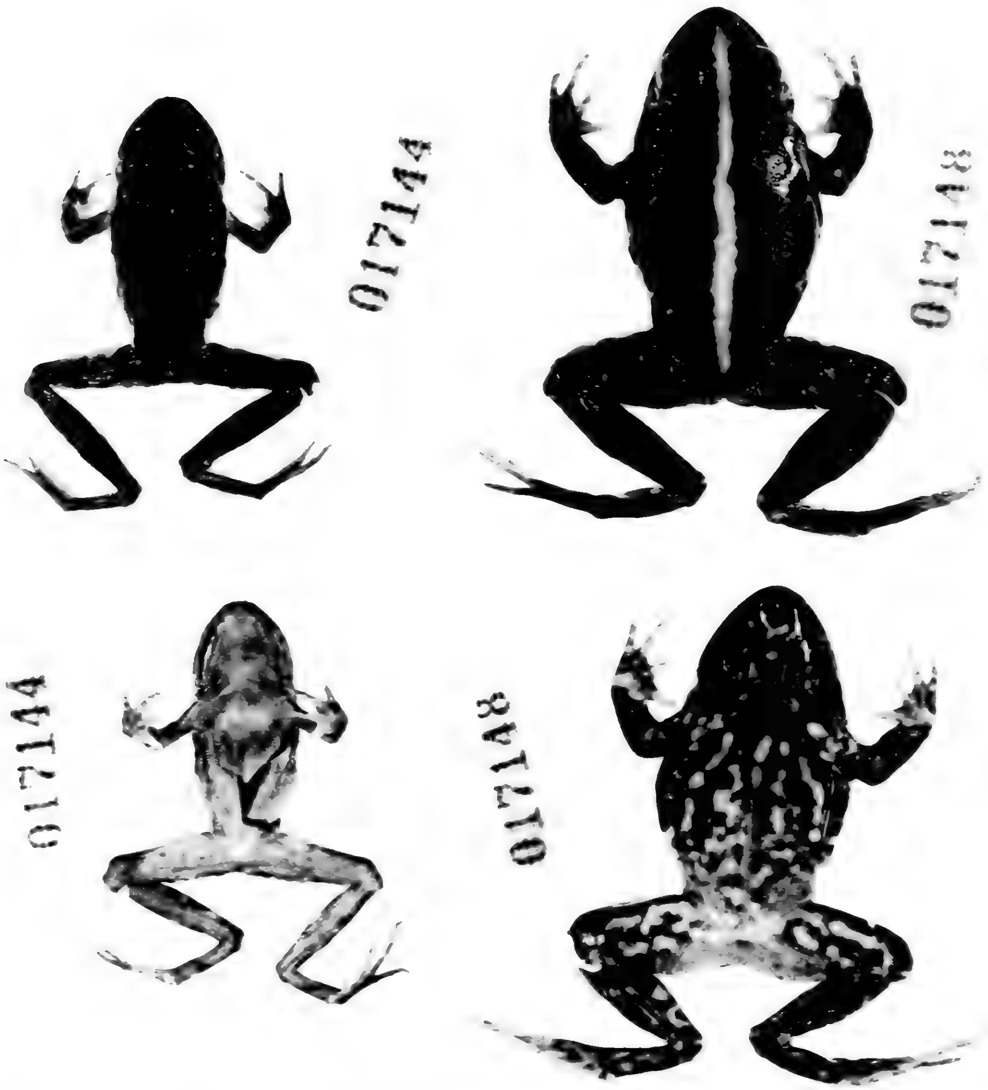

Fig. 3. Color pattern variation in *E. contulmoensis* (not to scale). Dorsal patterns (above) and ventral patterns (below) of the specimens MZUC 17144, 17148.

contulmoensis is dark purple dorsally with a rounded sternum. The upper part of the iris is bronze yellow in *E. contulmoensis* and the dorsal area is unmarked, while in *E. roseus* the upper part of the iris is orange and an hour-glass shaped mark is present on its dorsum. *Eupsophus contulmoensis, E. migueli* and *E. calcaratus* have a similar colored upper iris (bronze yellow), but these species differ in the ventral color and pattern. The belly of *E. migueli* is wine red with irregular white spots whereas the ventral area of *E. contulmoensis* is dark brown with bright yellow irregular spots. In *E. calcaratus* the spots are also present. On the other hand the dorsum of *E. migueli* and *E. calcaratus* exhibits a typical hour-glass pattern that is absent in *E. contulmoensis.*

Acknowledgments

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A NEW SPECIES OF COLUBRID SNAKE OF THE GENUS *CONIOPHANES* FROM THE HIGHLANDS OF CHIAPAS, MEXICO

Jonathan A. Campbell

Abstract.—A new species of colubrid snake, *Coniophanes alvarezi,* is described from the Meseta Central of Chiapas, Mexico. This snake inhabits temperate mesic pine-oak forest at elevations of 2012 to 2134 m. Unlike *C. alvarezi,* most other members of this genus have essentially lowland, tropical distributions. *Coniophanes alvarezi* is easily distinguished from its congeners by its uniformly brown dorsal coloration in adults (weakly striped in juveniles), immaculate venter, and features of lepidosis and dentition. This species appears to be most closely related to the wide-ranging *C. fissidens,* and a detailed comparison of these two species is presented.

Over 15 years have now passed since I first discovered an unusual colubrid snake of the genus *Coniophanes* near Teopisca in Chiapas, Mexico. On subsequent trips through the region (in 1976 and 1983) additional material representing this taxon was collected, including three eggs that were allowed to hatch. In all, a total of seven specimens are now available. I propose that this snake, apparently endemic to the Mexican state of Chiapas, be known as:

Coniophanes alvarezi, new species
Figs. 1–3

Holotype.—The University of Texas at Arlington (UTA) R-12256 (original field number, JAC 9389), an adult male from 11.3 km ESE Teopisca, 2073 m elevation, Chiapas, Mexico, collected by J. A. Campbell on 7 Aug 1983.

Paratypes.—Six specimens, all from Chiapas, Mexico: UTA R-2793, an adult female from 12.1 km ESE Teopisca, 2134 m elevation, collected 14 Aug 1973; UTA R-5766-67, adult females from 10.3 km ESE Teopisca, 2012 m elevation, collected 16 Jun 1976; and UTA R-6111-13, two neonate males and a female, respectively, from 10.3 km ESE Teopisca, 2012 m elevation, that hatched on 18 Aug 1976 from eggs discovered beneath a log on 29 May 1976.

Diagnosis.—A relatively large species of *Coniophanes* in which females are known to reach 521 mm in total length; dorsal scales disposed in 19-19-17 rows; adults differing from all congeners in having a uniformly brown dorsal coloration and immaculate yellow venter (except for a few tiny black stipples anteriorly). All other members of the genus have at least traces of longitudinal body striping, except *C. lateritius* and some specimens of *C. meridanus,* both of which have an orange or red dorsal coloration and a black head or collar.

Description of holotype.—An adult male, 375 mm in total length; tail length 93 mm (24.8% of total); head length 14.9 mm from front face of rostral to posterior end of mandible; head width 8.5 mm at broadest point (level of angle of mouth); head moderately distinct from neck; snout acutely rounded in dorsal view; snout 2.3 times as long as horizontal distance across eye; pupil round; rostral about 1.7 times broader than high; head scutellation of generalized colubrid type; internasals 1.4 times wider than long, laterally contacting anterior and posterior

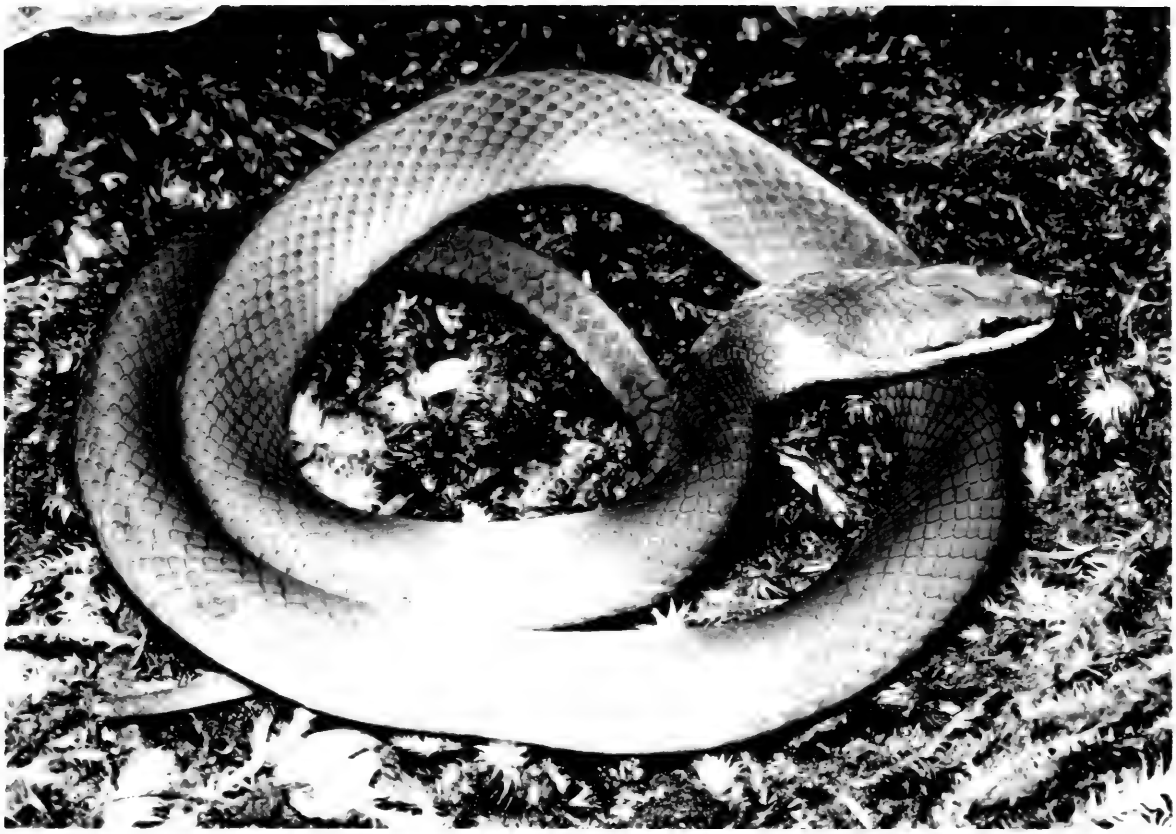

Fig. 1. Dorsal aspect of *Coniophanes alvarezi,* holotype, UTA R-12256, 375 mm TL.

nasals; prefrontals large, slightly longer than wide, laterally contacting posterior nasal and loreal, forming upper anterior margin of orbit; median prefrontal suture about half as long as frontal; frontal 1.6 times longer than wide; parietals about 1.6 times longer than wide, median suture slightly less than frontal length; nostrils located in central posterior portion of anterior nasals; loreal about half of combined length of nasals; two postoculars; temporals 1 + 2, separating supralabials 6 and 7 from parietal; supralabials 7/7, 1st contacting nasals and loreal, 2nd contacting loreal and preocular, 3rd contacting preocular and orbit, 4th contacting orbit and lower postocular, 5th contacting lower postocular and anterior temporal, 6th contacting primary and lower secondary temporals, 7th contacting lower secondary temporal; mental two times broader than long, separated from chinshields by first pair of infralabials which contact each other along the midline; anterior chinshields well developed, about twice as long as wide; posterior chinshields well differentiated from gulars, separated from 1st ventral by two gulars plus two preventrals; infralabials 9/9, 1–4 contacting anterior chinshields, 4th largest; dorsal scales disposed in 19 smooth rows, reduced to 17 posteriorly; dorsal scales in six rows at level of 10th subcaudal; no apical pits; ventrals 134; supra-anal tubercles (keels) present; anal divided; subcaudals 64, paired.

In life, dorsal ground color uniformly brown; venter immaculate pale yellow, except on the anterior third of the body where a small amount of fine black peppering present, especially on head and gular region; a black line running across upper portion of rostral and extending posteriorly just below eye to angle of mouth, thence posteriorly for two or three scales, bordered ventrally by white; supralabials mostly white, heavily speckled with black; iris copper-colored, with heavy suffusion of black ventrally.

In preservative (alcohol after formalin) ground color of dorsum brown, except where

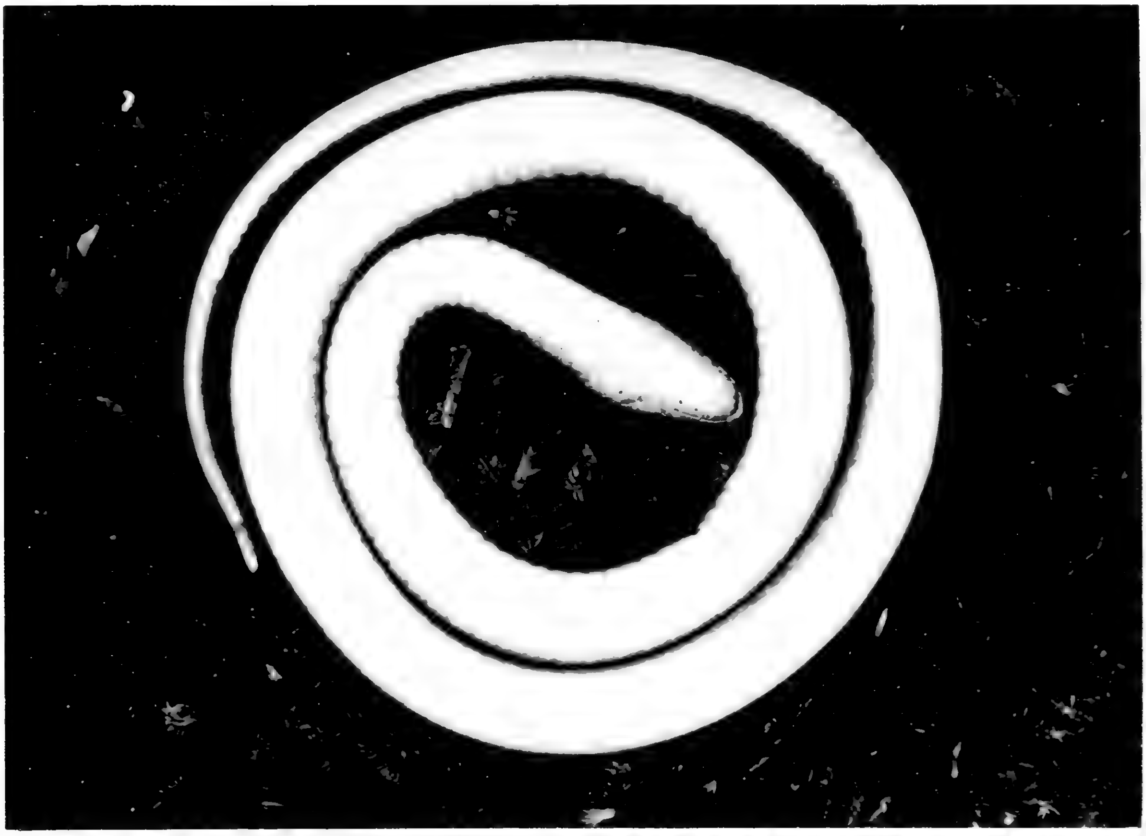

Fig. 2. Ventral aspect of *Coniophanes alvarezi,* holotype.

the stratum corneum sloughed off, where it is gray; venter creamy white.

Everted hemipenis five subcaudals in length; organ simple with sulcus spermaticus bifurcating at about level of subcaudal 3, but extending distally on capitulum for a length less than half of everted capitulum; asulcate, basal portion of organ possesses three large basal hooks, distal to which are some 7–9 large spines; sulcate side of organ also bears some 13–15 spines, but these are considerably smaller than those on the asulcate side; organ distinctly capitate; margin of capitulum covered with spinulate calyces, toward apex calyces become papillate; capitulum extends proximally almost half the length of organ on sulcate side; on asulcate side a pair of naked grooves extend distally from several large spines almost to apex (i.e., to overhang of the capitulum).

Variation.—The paratypic series is composed of two males and four females. The holotype is the largest male; the largest female has a total length of 521 mm, and a tail length of 111 mm (21.3% of total). Three juveniles, preserved on the date of hatching, were 154–162 mm in total length, with tail lengths of 34–38 mm (21.7–24.7% of total). Only one snake in the type series, an adult female, has an incomplete tail. The supralabials are invariably 7/7; the infralabials are 9/10 in one specimen, 9/9 in all others. The number of dorsal scale rows is 19-19-17 in all but one specimen which has 16 rows posteriorly. There are 134–136 and 140–143 ventrals, and 59–64 and 54–57 subcaudals, in males and females, respectively. The top of the head in the juveniles (UTA R-6111-13) is dark brown and contrasts with the pale brown of the dorsum. Juveniles have a faint middorsal stripe, darker than the ground color, involving only the vertebral scale row, extending the length of the body and tail, and have almost indistinguishable indications of a dark lateral stripe on scale row 4.

Fig. 3. Lateral aspect of *Coniophanes alvarezi* showing details of head pattern.

Etymology.—The name *alvarezi* is a patronym in honor of Miguel Alvarez del Toro, Director of the Instituto de Historia Natural of Chiapas. His noble love for the flora and fauna of southern Mexico has led to a better understanding of the natural history of Chiapan wildlife and forests and to the first significant conservation efforts taken in this state.

Distribution.—This species is known only from the Meseta Central of Chiapas at 2012 to 2134 m elevation. These highlands are covered by a temperate mesic pine-oak forest with abundant epiphytes. All specimens of *Coniophanes alvarezi* were taken under rocks or logs at the edges of clearings.

Comparison with Coniophanes fissidens.—Owing to characters of lepidosis, color pattern, hemipenes, and dentition, *Coniophanes alvarezi* appears to be most closely related to *C. fissidens.* The geographical distribution of *C. alvarezi* is more closely approached by that of *C. fissidens* than by any other species of *Coniophanes.* A comparison of selected features between *C. alvarezi* and *C. fissidens* is presented in Table 1.

Throughout most of its range *C. fissidens* usually has 21 dorsal scale rows at midbody (Bailey 1939, Minton & Smith 1960, Smith 1941). However, several isolated populations of *C. fissidens* in the northern part of the range have a modal number of 19 dorsal scale rows at midbody. The populations of *C. fissidens* inhabiting eastern San Luis Potosí and west-central Veracruz, described as *C. f. proterops* (Smith, 1941) and *C. f. convergens* (Shannon & Smith, 1949), resemble *C. alvarezi* in usually having 19 midbody dorsal scale rows and 7 supralabials. These snakes also have a relatively high number of ventrals for the species (males, 121–133; females, 126–133) and low number of subcaudals (males, 63–80; females, 59–74) (Smith 1941; Smith & Laufe 1945; Taylor 1949, 1953), but the counts do not overlap the range of variation known for *C. alvarezi.* The pattern of longitudinal body striping is relatively subdued, but always present, at least posteriorly, in adults (Smith 1941; Taylor 1949, 1953), and is distinct in juveniles and subadults (Smith 1941). *Coniophanes f. proterops* was reported from high elevations of the Atlantic versant of Chiapas by Smith & Williams (1963) on the basis of three specimens from two localities, 13 miles east of Las Rosas and Monserrat. I have not re-examined these specimens, housed in the University of Illinois Museum of Natural History, but the description provided by these authors is similar in some respects to *C. alvarezi,* although the ventral and subcaudal counts suggest they may be all males rather than females as stated.

Specimens of *C. fissidens* from the Pacific slopes of Michoacán and Guerrero, described as *C. f. dispersus* (Smith, 1941), also have 19 midbody scale rows (Bailey 1939, Davis & Dixon 1959, Peters 1954, Smith 1941), but in most other respects of lepidosis and pattern do not closely resemble *C. alvarezi.*

Along the Atlantic versant of Middle America, *Coniophanes fissidens* occurs in well drained mesic forests from eastern San Luis Potosí and west-central Veracruz (Mexico) eastward across east-central Belize and northern Guatemala through Honduras, Nicaragua, Costa Rica, and Panama (Alvarez del Toro 1983, Henderson & Hoevers 1975, Lee 1980, Minton & Smith 1960, Myers 1969, Schmidt 1941, Shreve 1957, Stuart 1963, Wilson & Meyer 1985, Zug et al. 1979), but it is absent from most of the Yucatán Peninsula. *Coniophanes fissidens* also occurs along the Pacific versant from Michoacán and Guerrero (Mexico) eastward through Central America to Ecuador (Bailey 1939, Myers 1969, Peters 1954, Peters & Orejas-Miranda 1970, Smith & Taylor 1945, Zug et al. 1979). On the Pacific slopes this species has been reported from up to 1463 m in Mexico (Landy et al. 1966) and 1432 m in Guatemala (Campbell & Vannini 1988). I have taken two specimens of this species (UTA R-16015, 20744) on the Atlantic side of Guatemala in cloud forest at elevations of 1500–1600 m. The range of *C. fissidens* surrounds the highlands of the Meseta Central of Chiapas, but in no place is this species known to be sympatric with *C. alvarezi* or to attain similar elevations.

In a sample of 71 specimens of *C. fissidens* from southern Mexico and Guatemala (62 of Pacific slope origin, 9 from the Atlantic versant; Appendix), a number of salient differences are apparent between this species and *C. alvarezi* (Table 1). *Coniophanes alvarezi* differs from populations of *C. fissidens* in southern Mexico and Guatemala in having 19 midbody dorsal scale rows (vs. usually 21 in *C. fissidens*); 7 supralabials (vs. usually 8–9); usually 9 infralabials (vs. 10–11); 134–136 and 140–143 ventrals in males and females, respectively (vs. 114–124 and 119–131, respectively); 59–64 and 54–57 subcaudals in males and females, respectively (vs. 67–86 and 59–86, respectively); a uniformly brown or brownish olive dorsum in adults (vs. dark lateral and usually middorsal stripes); an essentially immaculate yellow venter (vs. a white or cream colored venter, heavily marked with dark spots, speckling, or mottling); and a relatively short tail that accounts for 22.8–24.8% and 20.9–21.7% of the total length in males and females, respectively (vs. 29.3–35.4% and 25.5–33.8%, respectively).

Coniophanes fissidens from the Atlantic versant of southern Mexico and Guatemala often possess large prominent dark spots on the lateral edges of the ventrals; the venter of snakes from Pacific Chiapas and Guatemala is heavily strippled or flecked with black anteriorly, less so posteriorly.

The vague dark stripes in juvenile *C. alvarezi* are not positioned the same as in *C. fissidens,* but may have been derived from the pattern evident in the latter species. The color pattern in juvenile *C. alvarezi* consists of a poorly indicated dark strip confined to

Table 1.—Comparison of *Coniophanes alvarezi* and *C. fissidens* from southern Mexico and Guatemala for selected features of lepidosis, color pattern, and proportion. These data are based on specimens examined (see Appendix).

	Coniophanes alvarezi	*Coniophanes fissidens*
Dorsal scale rows	19–19–17(16)[1]	21(19)–21(19)–17(15)[2]
Supralabials	7 (100)%	7 (0.7%) 8 (97.9%) 9 (1.4%)
Infralabials	9 (93.0%) 10 (7.0%)	9 (12.7%) 10 (86.6%) 11 (0.7%)
Ventrals (males)	134–136 ($\bar{x}$ = 135.3)	114–124 ($\bar{x}$ = 119.2)
(females)	140–143 ($\bar{x}$ = 141.3)	119–131 ($\bar{x}$ = 124.7)
Subcaudals (males)	59–64 ($\bar{x}$ = 62.3)	67–86 ($\bar{x}$ = 77.5)
(females)	54–57 ($\bar{x}$ = 55.7)	59–86 ($\bar{x}$ = 73.0)
Adult dorsal color pattern	Uniformly brown or brownish olive	With distinct dark lateral stripes; often with dark dorsal stripe
Ventral color pattern	Immaculate yellow, except for a few dark flecks in gular region	Usually white or cream, with dark spots or mottling on lateral portion of ventrals
Tail/total length (males)	22.8–24.8% ($\bar{x}$ = 24.1%)	29.3–35.4% ($\bar{x}$ = 33.1%)
(females)	20.9–21.7% ($\bar{x}$ = 21.3%)	25.5–33.8% ($\bar{x}$ = 30.9%)

[1] The dorsal scale rows are reduced posteriorly to 16 in one paratype (UTA R-2793).

[2] In 5 of 62 specimens examined from the Pacific versant of Guatemala and southern Mexico, the number of dorsal scale rows is reduced to 19 anteriorly and/or at midbody; one of nine specimens from the Atlantic slopes of southern Mexico and Guatemala has 19 dorsal scale rows at midbody. Only one specimen (UTA R-20711) from a large series collected at Finca El Faro, Quezaltenango, Guatemala, has 15 dorsal scale rows posteriorly.

the vertebral scale row and extremely faint darker lateral stripes on scale row 4. The dark coloration on the dorsum of *C. fissidens* extends over 3 to 7 dorsal scale rows, including the vertebral row, and the lateral stripes are broad, extending from scale rows 1 to 5, with particularly dark pigment on the upper portion of scale row 4 and the lower portion of scale row 5.

The hemipenes of *Coniophanes fissidens* differ from those of *C. alvarezi* in that on the asulcate side of the organ the distal most spines are nearly as large or larger than the basal hooks, and in that there is no pair of naked grooves.

In a paratype of *C. alvarezi* (UTA R-5767) the right maxillary bone bears 9 teeth (counting sockets), followed by a broad diastema and two enlarged fangs with deep anterolateral grooves extending four-fifths of their length. The right palatine and pterygoid bones have 7 and 21 teeth, respectively. Examination of the dentition and associated bones of ten specimens of *C. fissidens* from Quezaltenango (Guatemala), only some 150 km frm the type locality of *C. alvarezi,* reveals a number of differences. In comparison with *C. fissidens,* the teeth are relatively shorter, stouter, and not so strongly recurved; the choanal process of the palatine and the ectopterygoid process of the maxilla are more broadly expanded; and the ectopterygoid is more robust in *C. alvarezi.* There are 13–14 maxillary teeth (including the enlarged posterior teeth), 9–11 palatal teeth, and usually more than 21 pterygoid teeth in *C. fissidens.* The two posterior maxillary teeth of *C. fissidens* have strikingly different grooves from *C. alvarezi.* In *C. fissidens* the groove is very wide at the base of the tooth and tapers distally; in *C. alvarezi* the groove is no wider proximally than distally. Further, the tips of the rear maxillary teeth in *C. fissidens* become distinctly compressed and bladelike, whereas in *C. alvarezi* the tips of these teeth are only slightly modified.

Comparisons with other species of Coniophanes.—Other than *C. alvarezi,* only two species of *Coniophanes* may lack any trace of longitudinal body striping. *Coniophanes lateritius* occurs in the Pacific Mexican lowlands and foothills from Sinaloa (Hardy & McDiarmid 1969) to Oaxaca (Smith & Taylor 1945). This species has a black head or collar and a red dorsum, often becoming dark posteriorly (Hardy & McDiarmid 1969, Smith & Grant 1958). *Coniophanes lateritius* further differs from *C. alvarezi* in having usually more ventrals (140–146) and subcaudals (84–99). *Coniophanes meridanus* has a uniclor reddish dorsum, pale temporal stripes, an incomplete black collar, often a trace of a middorsal stripe, and a bifurcate spineless hemipenis that extends 11 subcaudals (Bailey 1939). Pale temporal stripes are present in *C. imperialis, C. piceivittis,* and *C. schmidti,* and the latter two species have a broad dorsal black band. A double row of conspicuous black spots is present on the ventrals of *C. bipunctatus* and *C. quinquevittatus. Coniophanes bipunctatus, C. piceivittus, C. quinquevittatus,* and *C. schmidti* usually have 21 or more dorsal scale rows at midbody, *C. meridanus* and *C. joanae* have 17. The number of ventrals is higher in *C. piceivittus* (153–174), *C. quinquevittatus* (152–163), and *C. schmidti* (158–175), and lower in *C. joanae* (131–132). *Coniophanes alvarezi* has fewer subcaudals (54–64) than any congener except *C. joanae* (47± 53) and, very rarely, specimens of *C. imperialis* (62–94) and *C. quinquevittatus* (63–70). *Coniophanes dromiciformis* is a striped South American species and is not considered here.

The only other named species of *Coniophanes* with an essentially upland distribution is *C. joanae,* known from mesic montane forests in Panama east of the canal at elevations of 500–1440 m (Myers 1966, 1969). This species differs from *C. alvarezi* in having a brown venter and supralabials, longitudinal body striping, and 17 dorsal scale rows at midbody. *Coniophanes bipunctatus, C. imperialis, C. meridanus, C. quinquevittatus,* and *C. schmidti* are restricted to lowland habitats and their range includes the northern portion of the Yucatán Peninsula (Duellman 1965, Lee 1980, McCoy 1969, Smith 1960). At least two of these species, *C. bipunctatus* and *C. quinquevittatus,* are semiaquatic and found in swampy or coastal lagoon habitats (Conant 1965, McCoy 1969, Myers 1969).

Resumen

Se describe una nueva especies de colúbrido, *Coniophanes alvarezi,* de la Meseta Central de Chiapas, México. Esta especies de culebra occure en los bosques húmedos de pino y encino a elevaciones de 2012 a 2134 msnm. Al contrario de *C. alvarezi,* los otros miembros del género tiene rangos tropicales en tierras bajas. Se distingue facilmente *C. alvarezi* de sus congéneres por su coloración, color dorsal uniforme, su vientre sin manchas, y características de escamación y dentición. Parece que esta especie está relacionada con *C. fissidens* que tiene un rango muy extensivo, y se presenta una comparación detallada de estas dos especies.

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Appendix

Specimens of Coniophanes fissidens *examined.*—All are in the University of Texas at Arlington Collection of Vertebrates.

Guatemala: Baja Verapaz; vicinity of La Unión Barrios, 1500–1600 m (UTA R-16015, 20744); Escuintla: S slope Volcán de Agua, Finca Rosario Vista Hermosa (UTA R-4468, 16016, 20691); Izabal: 5.1 km WSW Puerto Santo Tomás, 152 m (UTA R-20684); 7.0 km SW Puerto Santo Tomás, 400 m (UTA R-20685); Quezaltenango: S slope Volcán Santa María, ca. 4.0 km N El Palmar, 875 m (UTA R-20692-743); Finca El Carmen (UTA R-20686-90).

Mexico: Oaxaca; Cerro Baúl, 19 km NW Rizo de Oro (UTA R-12257); 2–3 mi S Tapanatepec (UTA R-4337, 4339); Veracruz; 2.1 mi NW Sontecomapan (UTA R-3069); 7.7 mi NW Sontecomapan (UTA R-9457, 9468); 5.6 mi ESE Tebanca (UTA R-3067).

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THE KARYOTYPE OF *EXILIBOA PLACATA* BOGERT (TROPIDOPHEIDAE), AND COMPARISONS WITH THE FAMILY BOIDAE (REPTILIA: SERPENTES)

Laurence M. Hardy

Abstract.—The first karyotype for any member of the Tropidopheidae is described from one male and one female of the dwarf boa, *Exiliboa placata* Bogert, from Oaxaca. The diploid number is 36, composed of 16 macrochromosomes and 20 microchromosomes. A possible secondary constriction is present on the second pair of macrochromosomes, and this constitutes the only distinctive difference between this species and some members of the Boidae. The significance of possible differences in centromere positions between *Exiliboa* and boids with 36 chromosomes is unknown.

The Tropidopheidae includes four genera according to several recent authors (Underwood 1976, McDowell 1987): *Tropidophis* (15 species), *Trachyboa* (2 species), *Ungaliophis* (2 species), and *Exiliboa* (monotypic). Nothing is known of the chromosome morphology for any member of the family. This paper reports the karyotype of the monotypic genus *Exiliboa.*

Two specimens of *Exiliboa placata* Bogert were available for study: an adult female (UTA R-4731) and an adult male (UTA R-4732). These specimens were collected by Jonathan A. Campbell at 7.1 mi. (UTA R-4731) and 6.5 mi. (UTA R-4732), respectively, north of the crest of Cerro Pelón, Oaxaca, México, on 28 June 1975.

Chromosomes were prepared by the hypotonic citrate method of Patton (1967), using the modification by Cole & Leavens (1971). Velban was used instead of colchicine. Each macrochromosome was measured (to the closest 0.01 mm) with dial calipers directly on the 4×5" negative. Chromosome terminology follows Cole (1970). The arrangement of the chromosomes within the karyotype is based on size, from the largest pair (number one) to the smallest. In addition to the karyotypes presented (Figs. 1, 2), I subjected the measurements of the best 19 cells (seven cells from the female and twelve cells from the male) to computer analysis using the program Karypak (ver. 1.0) by William H. LeGrande (pers. comm.). The macrochromosome means were calculated from each arm of each chromatid. In this analysis only macrochromosomes were measured and, for purposes of the karyotype percentages and arm ratio (centromeric index) estimations, they were treated as the entire complement (i.e., microchromosomes were not included as part of the karyotype). This process does not allow for the detection of differences among the microchromosomes nor for the contribution of the microchromosomes to the entire karyotype. However, for most snakes such information on the microchromosomes is rarely available and any differences in size are suspect, in most cases, because of the small sizes and poor resolution. Therefore, omission of the microchromosomes is practically the same as assignment of a constant. I believe that this approach is most effective and reasonable for the critical examination of the macrochromosomes. Since no sexual dimorphism was detected, the male cells were combined with the female cells for the construction of the composite idiogram (Fig. 3).

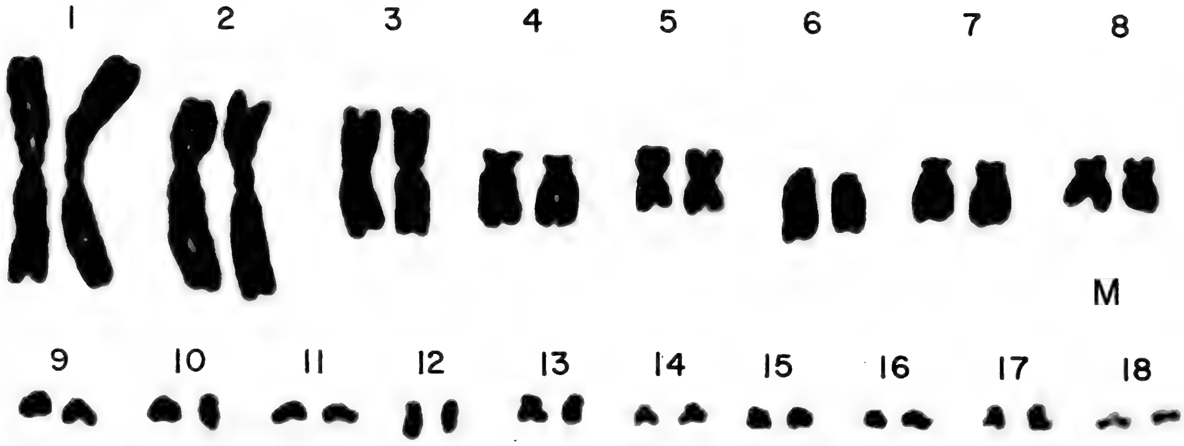

Fig. 1. Karyotype of an adult male *Exiliboa placata* (UTA R-4732), 2n = 36.

Fifteen cells each from the male and the female were photographed. The karyotype consists of eight pairs of macrochromosomes and ten pairs of microchromosomes for a diploid number of 36 (Figs. 1, 2). The fundamental number is 56 (30 from macrochromosomes and 26 from microchromosomes). The largest macrochromosome pair is metacentric, the second largest pair is submetacentric, and pair three is metacentric. These three pairs are clearly distinguishable from all of the other chromosomes. Pairs four and seven are subtelocentric and similar in morphology, but pair seven is slightly smaller and the short arms are slightly longer (proportionally; Table 1) than the short arms of pair four. Pair five is metacentric, pair six is telocentric, and pair eight is submetacentric. All of the macrochromosomes are easily distinguishable from each other and from all of the microchromosomes (Fig. 3). At least three pairs of the microchromosomes appear to be bi-armed; the remainder appear to be telocentric, or nearly so. No morphologically distinguishable sex chromosomes are apparent; however, pair five is probably homologous to the ZZ sex chromosomes because it is the only pair of metacentric macrochromosomes that is approximately the same size as the ZZ sex chromosomes identified in members of the Boidae by other workers (Mengden & Stock 1980). All other macrochromosomes of *Exiliboa* are distinctly different in centromere position or in size.

Comparisons with the Boidae.—All species of the Boidae for which karyotypes are known have 36 chromosomes (2n) ex-

Fig. 2. Karyotype of an adult female *Exiliboa placata* (UTA R-4731), 2n = 36. The arrow indicates a possible secondary constriction.

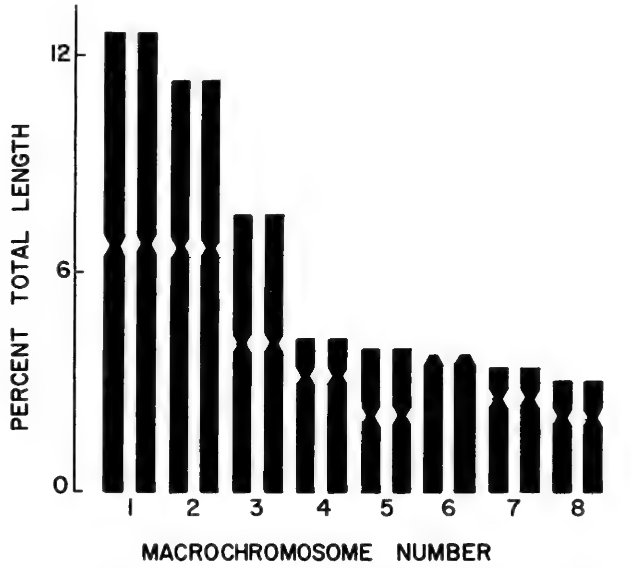

Fig. 3. Composite idiogram of the macrochromosomes of *Exiliboa placata,* based on mean measurements and arm ratios from 19 cells. Percent total length is calculated from the total length of the macrochromosomes in each cell, excluding the ten pairs of microchromosomes. Macrochromosome number is the pair number.

Table 1.—A comparison of the macrochromosomes of *Exiliboa placata,* both sexes combined; n = 19. Percent of total is the percent of the total length (in mm, measured from the 4 × 5″ negatives) of macrochromosomes, excluding the microchromosomes.

Pair number	Arm lengths			Percent of total	Centromere position
	Short	Long	Ratio		
1	12.2	14.3	1.17	12.62	Metacentric
2	9.6	14.1	1.47	11.29	Submetacentric
3	7.5	8.5	1.13	7.62	Metacentric
4	2.1	6.8	3.24	4.24	Subtelocentric
5	4.0	4.4	1.10	4.00	Metacentric
6	0.0	7.8	0.00	3.71	Telocentric
7	1.8	5.5	3.06	3.48	Subtelocentric
8	2.1	4.3	2.05	3.05	Submetacentric

cept *Sanzinia madagascarensis* (Branch 1980), *Acrantophis dumerili* (Mengden & Stock 1980), *Eryx johni* (Singh et al. 1968), and *Gonglyophis conicus* (Singh et al. 1970), all with 34, *Corallus caninus* with 44 (Beçak 1965), and *C. enhydris* with 40 (Gorman & Gress 1970).

Diploid numbers other than 36 among boids probably represent derived conditions since 36 is the modal number for known boids and is also represented in the primitive *Boa* (McDowell 1979). In *Sanzinia madagascarensis* there are nine pairs of macrochromosomes, including an extra metacentric (pair four in Mengden & Stock 1980:fig. 10), but only eight pairs of microchromosomes, versus ten in *Exiliboa. Acrantophis dumerili* differs from *Exiliboa* by having only nine pairs of microchromosomes; the macrochromosomes appear indistinguishable except for the telocentric W chromosome in *Acrantophis* (Mengden & Stock 1980). *Eryx johni* differs from *Exiliboa* by having pair eight telocentric, not submetacentric, and by having only nine pairs of microchromosomes, all of which are telocentric (Singh et al. 1968); at least three pairs of microchromosomes in *Exiliboa* are bi-armed. The species of *Corallus* have telocentric macrochromosomes, probably due to centric fission of the first two (*C. enhydris*) or four (*C. caninus*) macrochromosomes. *Gonglyophis conicus* has one fewer microchromosome (2n = 34; Singh et al. 1970).

All of the remaining boids for which chromosome morphology is known have diploid numbers of 36. The macrochromosomes of *Exiliboa placata* are similar to those reported for *Liasis* by Mengden & Stock (1980) except that pair six of *Exiliboa* is clearly telocentric and distinguishable from all other pairs, whereas pairs six, seven, and eight of *Liasis* are telocentric; Mengden & Stock (1980) also identified pair five as ZZ of the sex chromosomes. *Python molurus* differs from *Exiliboa* only in the arm ratios of some macrochromosomes (Singh et al. 1968). The karyotype of *Xenopeltis unicolor* (sometimes included in the Boidae) is similar to *Exiliboa* in number and morphology of chromosomes except that pairs four, seven, and eight have longer short arms than do the apparent homologues in *Xenopeltis* (Cole & Dowling 1970). Also similar in number and morphology is *Loxocemus bicolor* (Fischman et al. 1972). In *Charina bottae* and *Lichanura roseofusca* the karyotypes (Gorman & Gress 1970) are extremely similar to *Exiliboa* except that the telocentric macrochromosome (pair six in *Exiliboa*) appears homologous to the smallest macrochromosome pair in *Charina* and *Lichanura* and pairs five through seven in *Charina* and *Lichanura* are telocentric rather than subtelocentric (pairs four and seven) or even submetacentric (pair eight) as in *Exiliboa.* The microchromosome morphology was not given by Gorman & Gress (1970) although they did report a fundamental number of 44, which only would result from all of the microchromosomes being treated as telocentric. *Eunectes murinus, Epicrates cenchria,* and *Boa constrictor* differ from *Exiliboa* mainly by having relatively shorter short arms on macrochromosomes four (pair five in Beçak 1965:figs. 1–12), seven, and eight (Beçak 1965). Examination of additional tropidopheids is necessary to determine the significance of the above differences.

Even though heteromorphic sex chromosomes are not evident in *Exiliboa,* pair five is probably homologous to the ZZ sex chromosomes identified in some boids (*Acrantophis* and *Liasis* by Mengden & Stock 1980). The lack of apparent difference among the cells studied here suggests that the W sex chromosome has undergone little, if any, morphological change if homomorphic sex chromosomes are primitive in snakes (Beçak et al. 1966). This supports the position that *Exiliboa* is relatively primitive, among snakes in general, and its close relationship to the boids is not unreasonable.

In at least five (three from the male, two from the female) of the photographs of *Exiliboa* chromosomes there is a consistent discontinuity in the basal part of the short arm of chromosome pair two (Fig. 2). That discontinuity is possibly a secondary constriction; if so, it is the first reported for any member of either the Tropidopheidae or the Boidae.

The karyotype of *Exiliboa placata* is not distinctively different from several species of the Boidae, nor is it distinctive from several non-boids (i.e., *Xenopeltis* in the Xenopeltidae [Cole & Dowling 1970]; several colubrids, except for heteromorphic sex chromosomes in some colubrids). However, consistent differences in centromere positions (i.e., pairs 4, 7, and 8 with longer short arms in *Exiliboa*) might exist between *Exiliboa* and some boids with 36 chromosomes. Based on the karyotype alone, the evolutionary relationships of *Exiliboa* within the Tropidopheidae and the separation of the Tropidopheidae from the Boidae is neither refuted nor supported.

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RHODOGORGON, AN ANAMOLOUS NEW RED ALGAL GENUS FROM THE CARIBBEAN SEA

James N. Norris and Katina E. Bucher

Abstract.—*Rhodogorgon* (Rhodophyta) a new genus with two species, *R. carriebowensis* and *R. ramosissima,* superficially resembling some gorgonian soft corals, is described from the Caribbean Sea. Studies of vegetative morphology, male reproductive structure, pigment composition, nature of calcium carbonate, and ultrastructure reveal a combination of characters that is exceptional among the red algae: thallus with a sharply demarcated cortex of laterally interconnected cortical fascicles and rhizoidal filamentous medulla; three types of cortical cells which develop from the base of a cortical fascicle—1, pigmented, assimilatory filaments with inflated, hyaline apical cells, 2, unusual elongate, hyaline, hair-like calciferous cells with inflated tips, and 3, basal hair cells; uninucleate vegetative cells that lack secondary pit-connections and cell fusions; pit-plugs with two cap layers on either side of plugs, the outer caps dome-shaped; and calcite (among the red algae previously known only in the Corallinales) confined to single "husklike" structures (unique among all algae) that distally surround a calciferous cell. Thalli are apparently dioecious; spermatangial parent cells are borne bilaterally on subterminal cells of the cortical filaments, with each cutting off a single spermatangium by oblique division. Possible taxonomic affinities of the new genus are discussed.

A relatively large, cartilaginous, and peculiar red alga has been collected at many Caribbean localities over the past 16 years. Plants are usually rare or sparse in occurrence and grow in shallow to mid-subtidal depths on rocks or coral heads, in patch reefs, fringing reefs and barrier reefs throughout the year. This alga could have been easily overlooked because of its resemblance to some gorgonians (Gorgonacea; Anthozoa) in shape, color, and thick cartilaginous texture (see color photograph of "mystery alga" in Littler et al. 1989:184). It has been noted by F. M. Bayer (octocoral systematist) that the living plants of *Rhodogorgon carriebowensis* superficially resemble some species of *Carijoa* F. Müller (a gorgonian cosmopolitan in subtropical-tropical oceans), and the dried herbarium specimens of *R. ramosissima* resemble *Plumigorgia* Nutting (a gorgonian from the Indo-Pacific). Initial examination by our phycological colleagues suggested specimens could be confused with gorgonians. The presence of pit plugs between the exceedingly small cells, documented by TEM studies (S. Brawley, pers. comm.), demonstrated that the specimens were plants!

Materials and methods.—Specimens were collected from the Caribbean Sea, from 1973 to 1989 by skin or SCUBA diving, at depths from 1–25 m. For morphological studies, thalli were pressed fresh or preserved in 5% buffered Formalin/seawater. Collection numbers cited with the prefix JN- or KB- refer to the field notebooks of J. N. Norris or K. E. Bucher, respectively. Live specimens were studied in the field at the Smithsonian Institution's Carrie Bow Cay Laboratory on the barrier reef of Belize, the Galeta

Marine Laboratory of the Smithsonian Tropical Research Institute (STRI) on the Caribbean coast of the Republic of Panama, and aboard the NSF ships OR/V *Cape Florida* and OR/V *Columbus Iselin.*

Microscope slides for anatomical studies were prepared from living or liquid-preserved specimens by hand sectioning with single- or double-edged razor blades, or by using a Reichert Histostat cryostat microtome to make both transverse and longitudinal sections of the main axes, branches and apices. Some were acidified with 2–5% HCL to remove calcium carbonate, and then stained with aniline blue and mounted in serial dilutions of clear Karo Syrup with phenol added (as a preservative) following techniques of Tsuda and Abbott (1985), or acidified with 1–5% acetic acid and stained with aceto-iron-hematoxylin-chloral-hydrate (Wittmann 1965) and mounted in 50:50 Hoyer's mounting medium according to the procedure of Hommersand and Fredericq (1988). Other preparations of fresh or liquid-preserved specimens were not acidified or stained prior to mounting on microscope slides in order to observe the unique calciferous cells.

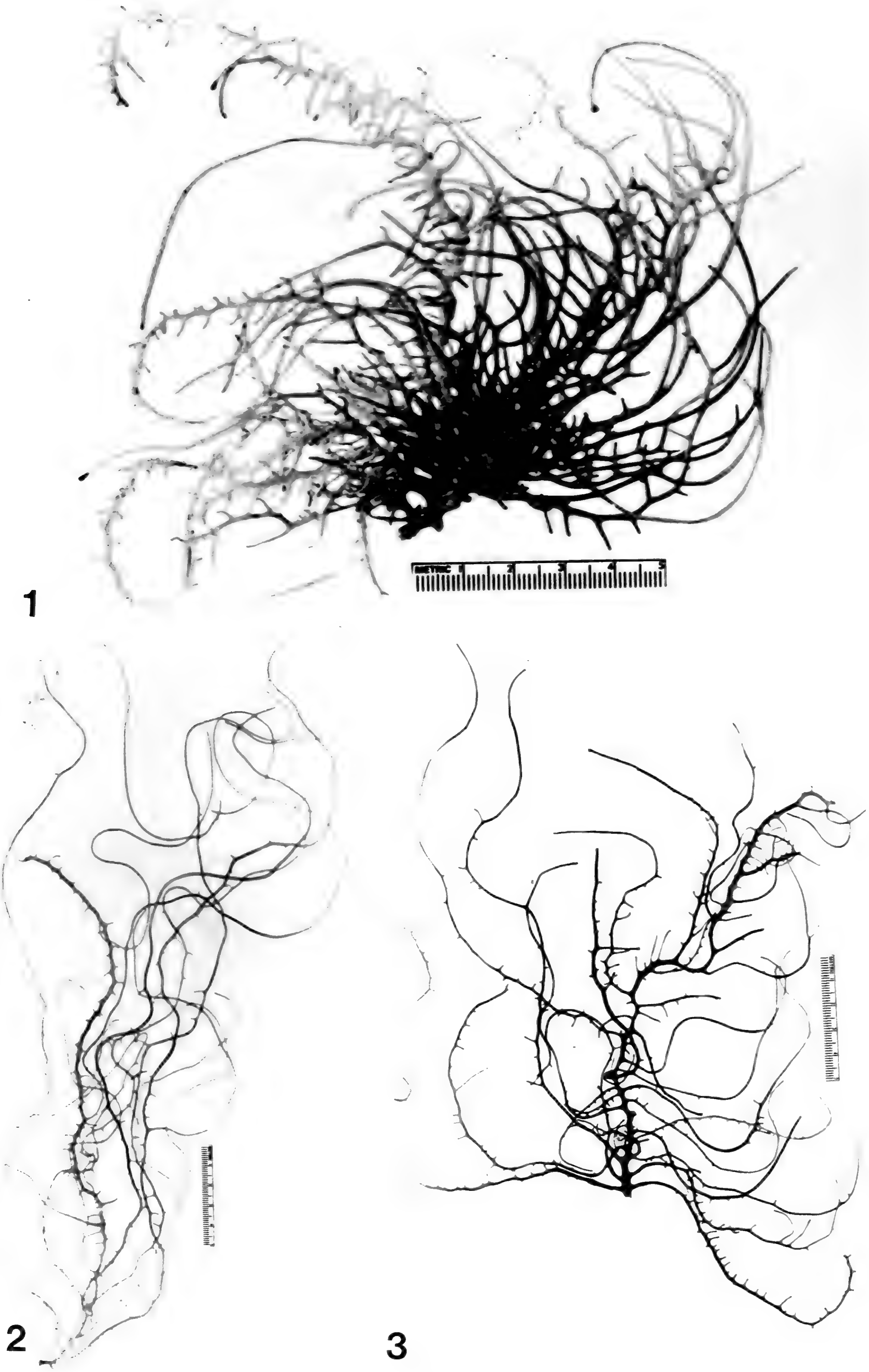
Living specimens of *Rhodogorgon* collected from patch-reefs in Belize (Carrie Bow Cay) and the Bahamas (Chub Cay) were returned to our laboratory and grown in the 511-liter algal reef tank, at 11D:13L photoperiod (under 6 Sylvania, 6 ft. VHO-160w fluorescent lights), a water temperature range of 26–29°C, and salinity range of 35.5–36.7‰. Field collected plants from Caribbean Panama (San Blas Islands) were grown in the outdoor holding tanks under natural conditions at STRI's Galeta Marine Laboratory from 1979–1984, and in the living coral reef exhibit (7570 liter) at the National Museum of Natural History under ten-1000w multi-vapor halide lights (Adey 1983) with other physical conditions similar to those described above in the 511 liter reef tank.

For ultrastructure studies, branches and main axes of freshly collected specimens were cut into 0.5–1.0 mm thick pieces and preserved in 5 dram vials of either 4% glutaraldehyde/seawater or 4% glutaraldehyde/cacodylate buffer, and then 2% osmium tetroxide (see previously described procedures in Pueschel 1979, 1980).

Freshly collected plants were frozen and transported in dark bottles covered with aluminum foil for pigment studies. Phycobiliproteins were extracted in 0.03 *M* Potassium-phosphate (pH 6.8) following the methods described by Gantt et al. (1979).

For calcification analysis, trans-sections 0.3–0.5 mm thick of the axes and branches of living and preserved specimens were placed on microscope slides. Some sections were rinsed in distilled water and others were not, then they were placed in glass petriplates and dried at 40°C in a Thomas drying oven or air-dried at room temperature. Calcium carbonate was analyzed by powder x-ray diffraction studies.

Comparative thin-layer chromatograms (TLC's) of 90% ETOH extracts of freshly collected specimens of *Rhodogorgon carriebowensis* from Carrie Bow Cay, Belize and *R. ramosissima* from Antigua were done at the Smithsonian's Carrie Bow Cay Lab. and aboard the OR/V *Cape Florida,* following methods of Norris & Fenical (1985). As part of a field research project aboard NSF's OR/V *Columbus Iselin* fresh homogenates of *R. carriebowensis,* collected from Chub Cay, Bahamas, were analyzed in collaboration with J. Burgess and R. Jacobs, for the presence of enzymes capable of producing bioactive compounds (i.e., phospholipase A and lipoxygenase). Lipoxygenase activity was measured both polarigraphically using a Clark type electrode and spectrophotometrically determining olefin conjugation utilizing arachidonic acid as substrate (Reddana et al. 1988). Phospholipase activity was measured directly based on procedures of Dagan and Yedgar (1987) using the fluorescent substrate 1-acyl-2-(N-4-nitrobenzo-2-oxa-1,3-diazole) aminocaproylphosphatidycholine, and separating the free fatty



Figs. 1–3. *Rhodogorgon carriebowensis,* from Carrie Bow Cay, Belize. 1, Holotype (US-098360). 2, A long, lax form with branches to 40 cm in length (US-098364). 3, A loose, lax form (US-098363).

acid product by solid phase extraction on C_{18} cartridges.

Type specimens, including microscope slides and liquid preserved material are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution. Additional cited specimens are deposited in ADU, BISH, MELU, MICH, UC and US (following herbarium designations of Holmgren et al. (1981).

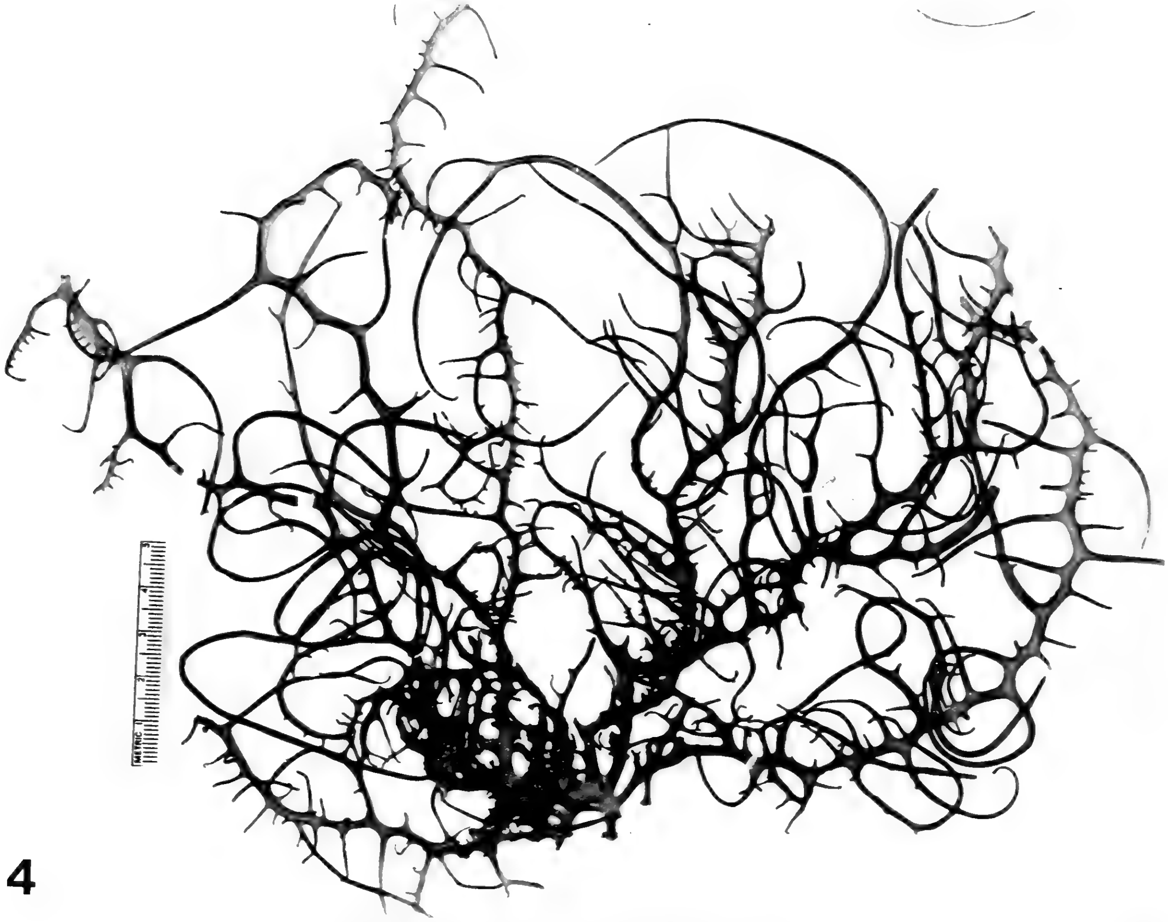
Rhodogorgon J. Norris et Bucher, gen. nov.

Description.—Thallus erectus rosealus vel atroruber, cartilaginogelatinosus, per hapteron tenue discoideum affixus, laxe vel abunde ramosus; ramis teretibus vel compressis. Frondes solitariae aut 2 aut 3 erectae orti stipite brevi; axibus principalibus 0.3–0.5 cm crassis, ramulis 2–3 mm crassis. Ramificatio strati corticalis ex fasciculis filorum pseudotrichomatorum aut pseudodichomatorum constans; medulla ex filis oblongatis eramosis rhizoidibus constans; rhizoidibus medullaris ab cellulis interioribus corticalibus ortis. Cellulae corticales et medullosae uninucleatae, conjunctionibus vegetativis et synapsibus secundis absentibus. Synapses primariae obturamentae cum duobus stratis capitularibus continentes, exterioribus tholiformibus. Extensio cellularum calcifera protoplasmica hyalina esegmentata cellulis interioribus fasciculorum corticalium orta, ad apicem cylindrica calcifera (calcite). Cellulae parentes spermatangiorum bilateraliter cellula subterminali filorum corticalium ortae, spermatangio singulo ferentes.

The thalli are erect, cartilaginous, slippery, locally lightly calcified, with terete to compressed upright main axes and side branches. Usually a single (rarely more) short stipe arises from a small, discoid holdfast. The thalli may be stringy and sparsely branched to a few orders, or compact and densely branched to several orders (Figs. 1–7). Branching is mostly irregular, or alternate, or more or less radial, or occasionally pinnate, and tends to become secund toward the apices.

The thalli apparently are multiaxial, consisting of two distinct regions, with a sharp boundary (Figs. 8, 9) between the pigmented, fasciculate cortical layer and the medulla of unpigmented, intertwined rhizoidal filaments (Figs. 8, 9). Both cortical cells (Figs. 11–13) and medullary cells (Fig. 17) are uninucleate and lack secondary pit-connections and cell fusions. The assimilatory filaments of the cortex are organized into fascicles that are radially interconnected at their base (Figs. 10, 11). The filamentous medulla is composed of hyaline, thick-walled rhizoidal filaments that interlace. One or two unpigmented medullary rhizoidal filaments are cut off secondarily from the innermost cortical cell bearing a cortical fascicle (Figs. 10–13). These rhizoidal filaments continue to grow inward, contributing to the structure of the medulla.

The branching pattern of a cortical fascicle is typically pseudotrichotomous, and there are three types of cortical structures. The first are filaments composed of pigmented, granular, cylindrical cells that terminate in an inflated hyaline cell (Figs. 16, 18, 21, 23–26). The second type are basal hair cells (Figs. 18–20), and the third are unique, elongate, unsegmented, hyaline, hair-like calciferous cells, which are distally surrounded by a brownish, "husk-like" calcareous structure (Figs. 21–26). A new branch within a cortical fascicle originates when a cell of a pigmented filament buds part of its cytoplasm distally (Figs. 13, 14). Subsequent septation of the protruded cytoplasm (Fig. 15) followed by cell division towards the thallus surface results in a new branch. The septum develops horizontally (Fig. 15) or slightly obliquely. The pseudotrichotomy of the cortical fascicle results when a cell that bears a pseudodichotomy buds (Fig. 13), septates, and undergoes cell division. Concordantly, a pseudodichotomy originates when the bearing cell of an unbranched cortical filament protrudes and



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divides (Figs. 14, 15). Well developed branches have a central branching point that has cut off rhizoids and bears two orders of trichotomies (Fig. 13). An unbranched cortical filament usually consists of 4–6 cells (Figs. 10, 11).

Cell division does not always produce a new side branch, but may stop after cutting off one cell that becomes the basal cell of a hair (Figs. 18, 19). Cytological transformation of such a basal cell is often accompanied by breakdown of its cell wall material, revealing persistent putative cellulose fibrils (Figs. 18, 19). Once the basal cell primordium becomes dense with cytoplasm and increases in size (Fig. 19), it cuts off a similarly darkly staining hair (Fig. 20) that protrudes beyond the cortical surface. If the hair is broken off, the pit-connection between the cells persists.

The specialized, brownish, "husk-like" structures of the calciferous cells are the localized sites of extracellular calcite precipitation. When dilute acid is pipetted underneath the coverslip, the calcite readily dissolves, revealing a hyaline, small to large, inflated tip on the elongate, unsegmented, hair-like cell. These hair-like cells are very thin, vacuolate protoplasmic extensions that are cut off and pit-connected to the base of a pseudotrichotomy (Figs. 24, 27) or pseudodichotomy (Fig. 26). The calcite completely surrounds the apical portion of the calciferous hair-like cell when it is narrow (Fig. 21), but as its tip inflates a longitudinal furrow (Figs. 22, 23) forms, and the narrow extension slightly expands in width (Figs. 24–26). Occasionally a very narrow channel forms within the cell wall of the hyaline, calciferous extension (Fig. 22). The calcite "husk-like" structures are scattered among and located just beneath the zone of the terminal inflated cells of the cortical filaments (Figs. 8, 9, 21, 23, 26). These unique calcite structures vary in abundance within the cortical layer and give a greyish sheen to the thallus. The calciferous cells are commonly one per fascicle, but up to three may be cut off. Segmentation within these calciferous cells was never observed, although their apical portions were occasionally separated from the remaining portion of the cell by a lenticular wall (Fig. 28).

Plants are apparently dioecious. In spermatangium bearing gametophytes, the cortex consists of a continuous zone of spermatangial parent cells (Fig. 29). Spermatangial parent cells are borne bilaterally on the subterminal cell of a cortical filament (Fig. 30), each cutting off a single spermatangium (Fig. 31) by oblique division.

Remarks.—*Rhodogorgon* is named for its resemblance to the branching soft corals, the gorgonians (Gorgonacea). *Rhodo-* means red and *-gorgon* refers to Gorgon, a figure in Greek mythology (Genaust 1976), and the other gorgons, Euryale, Steno and Medusa, who had hair of snakes.

Type species.—*Rhodogorgon carriebowensis.*

Key to the species of *Rhodogorgon*

1. Plants loose, sparingly branched to 2–3 orders, with determinate and indeterminate ultimate branches . . . . *R. carriebowensis*
– Plants more compact, densely branched to 3–5 orders, with determinate ultimate branchlets . . . . *R. ramosissima*

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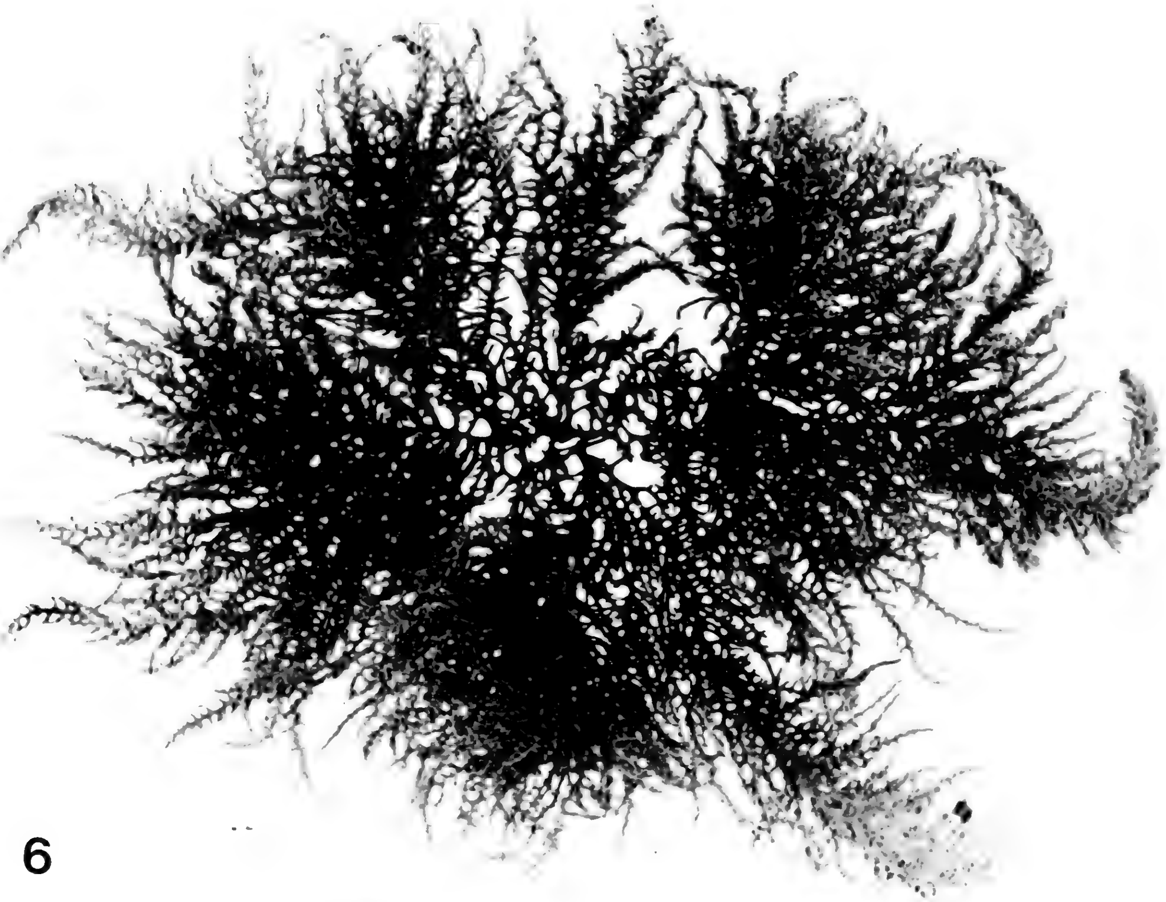
Figs. 4–5. Variation in branching of *Rhodogorgon carriebowensis.* 4, Specimen from Islas San Blas, Panama, with both long and short branches (US-098366). 5, Specimen from Passe du Marin, off Pte. Borgnesse, Martinique (US-098367).



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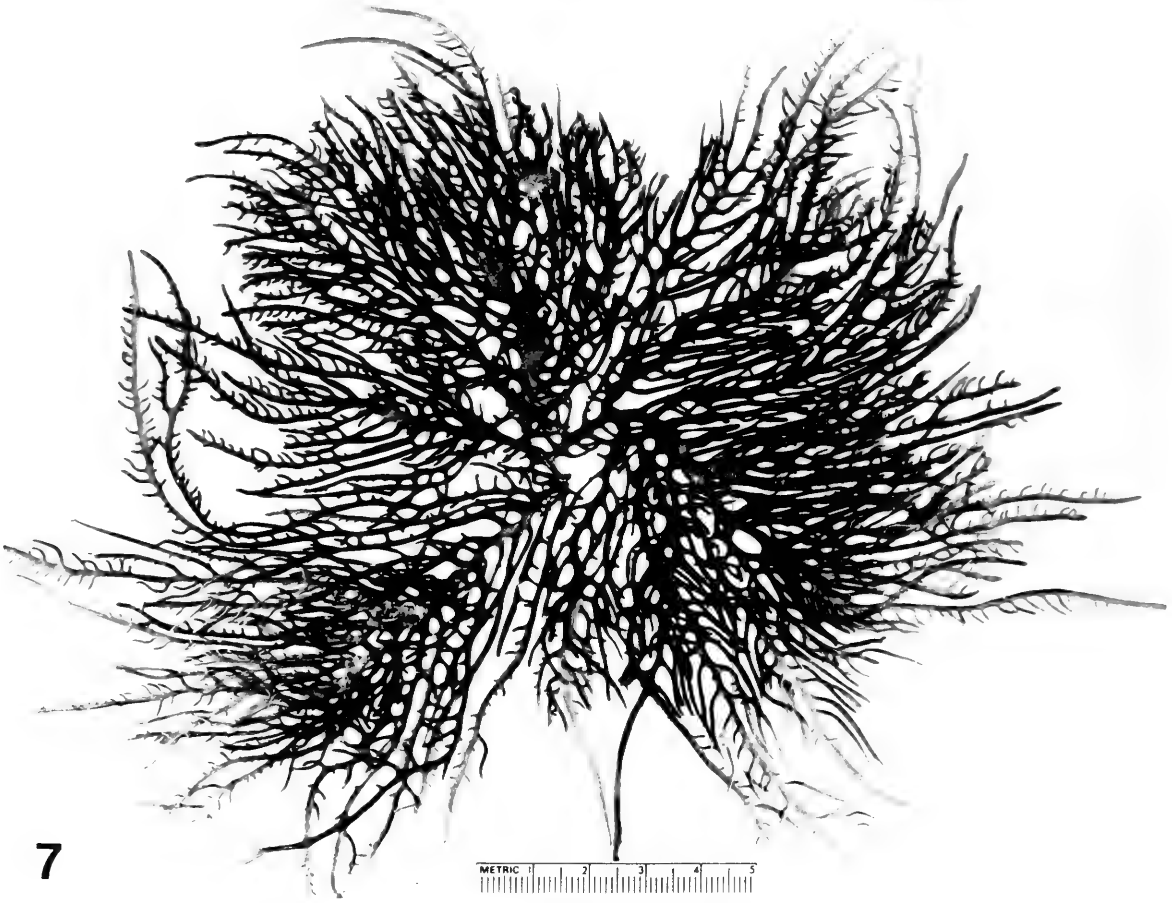

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Figs. 6–7. *Rhodogorgon ramosissima.* 6, Holotype from Carlisle Bay, Antigua (US-098361). 7, A more openly branched form, from Pte. Borgnesse, Martinique (US-098365).

Rhodogorgon carriebowensis
J. Norris et Bucher, sp. nov.
Figs. 1–5, 8–31

Diagnosis.—Thallus usque ad 50 cm, inferne atropurpureus, superne aurantio-rosealus. Frondes solitariae aut raro 2 aut 3, sparse vel profuse 1-2(-3)-plo ramosae; axibus ad 1.0 cm diam.; ramis saepe longis teretibus ad 6 mm diam. et 9.0–13.5(–40) cm longis; cellulis medullosis plusminusve 4.5 μm diam. et ad 90 μm longis; extensionibus calciferis 1–4 μm diam. et 40–65 μm longis, ad apicem calciferum 10 μm diam. et 25 μm longis.

The thalli are cartilaginous, slippery, to 50 cm tall, dark purple to light peach, usually darker below and lighter above, with a greyish tint throughout. A single (rarely two or three), short stipe grades into terete to compressed axes, to 1.0 cm diam. The axes branch irregularly, alternately, or occasionally more or less radially up to three orders. The branches are terete, short to long, to 6 mm diam. and up to 40 cm long (Fig. 2), with blunt ultimate branches to 4 mm diam.

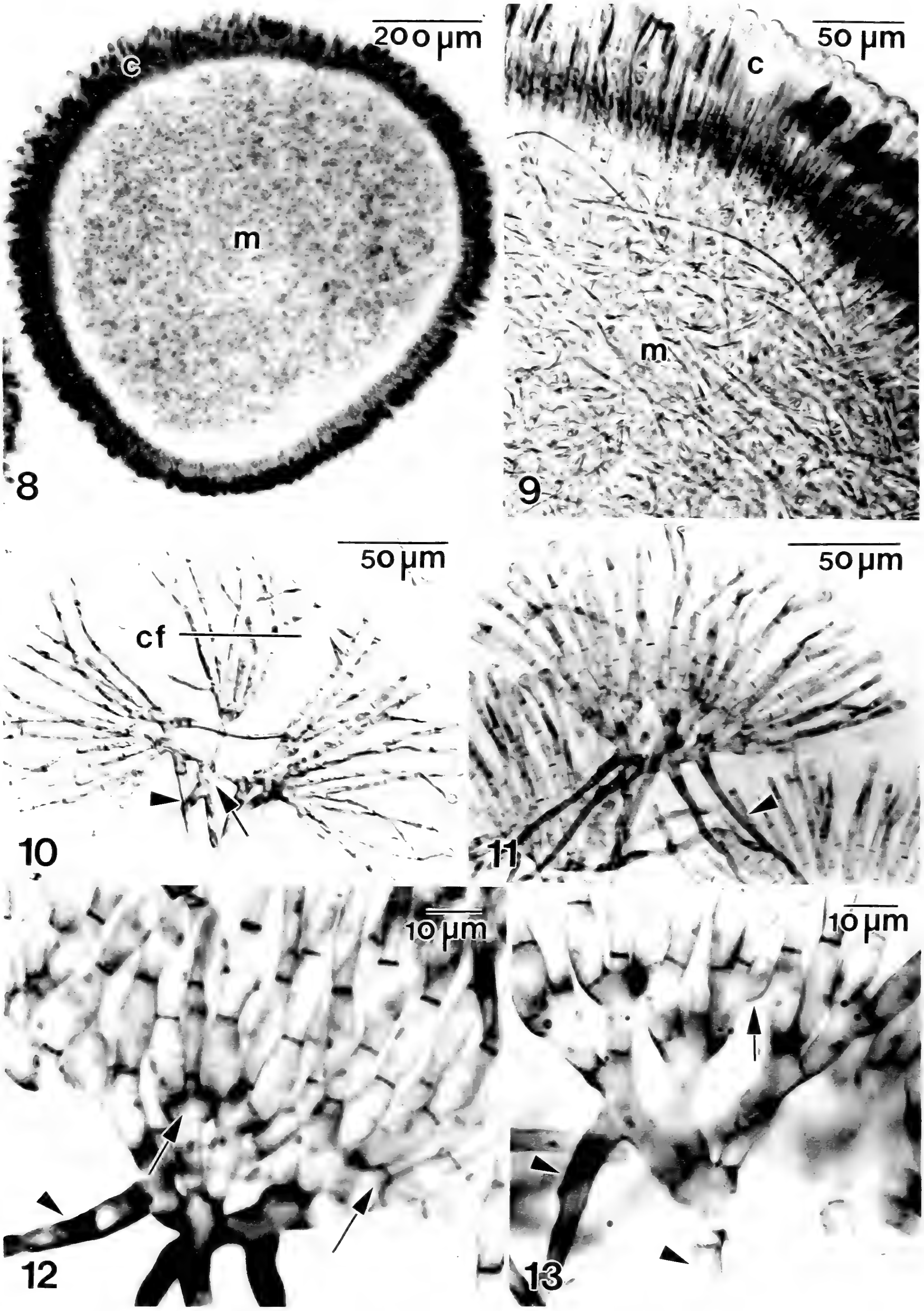
The cortex in cross section is 70–105 μm wide and distinctly separate from the medulla. Cortical filaments are composed of pigmented, granular, cylindrical cells, 1.5–6.0 μm diam. by 12–18 μm long, that terminate in bulbose, hyaline cells, 6–10 μm diam. by 9–14 μm long. The hyaline, calciferous cells are 1–4 μm diam. by 40–65 μm long, with a swollen tip, and bear unique, calcite structures distally, 10 μm diam. by 25 μm long. The medulla is composed of intertwined, hyaline, thin cells, 4 μm diam. and mostly to 90 μm long. All other characteristics are given above in the generic description.

Remarks.—*Rhodogorgon carriebowensis* resembles some species of the gorgonian *Carijoa.* It is named after Carrie Bow Cay, the type locality and site of the Smithsonian's Caribbean Coral Reef Ecosystem Program (CCRE) on the Belizean Barrier Reef. This species differs from *R. ramosissima* in being less densely branched and only to two or three orders, with the upper branches in some tending to be secund. The branches, including the ultimate branchlets, are either determinate or indeterminate, and sometimes are very long, to 40 cm. See *R. ramosissima* for other differences.

Type.—Carrie Bow Cay, Belizean Barrier Reef, Belize, spur and groove zone, 4.6–12.2 m depth, 1 May 1979, K. E. Bucher, JN-7520 (holotype: Alg. Coll. #US-098360).

Distribution.—Caribbean Sea: Bahamas, St. Croix, Belize, Martinique, Panama.

Paratypes.—Caribbean Sea: BAHAMAS.—Chub Cay, 4 m depth, among corals, 12 Jun 1989, R. Sims, s. n. (US). U.S. VIRGIN ISLANDS.—St. Croix: Boiler Bay, growing on fore-pavement in front of boiler, 3–4 m depth, 19 Aug 1978, W. Adey s. n. (US); Tague Bay, patch reef, 2.4 m depth, 6 Jan 1973, C. Bowman, IAA-11592 (MELU), 5 Apr 1973, P. Adey, IAA-11447a & b (BISH, US), and patch reef, 25 Jan 1974, R. Burke & R. Steneck, IAA-11783 (MICH, US). BELIZE.—W of Carrie Bow Cay, patch reef, among gorgonians and corals, 4.6–6.1 m depth, 25 Nov 1980, K. Bucher & R. Sims, JN-10670 (UC); off S end of Carrie Bow Cay, on coral head, 4.5 m depth, 30 Mar 1980, M. Hay, RHS-80-275, and 6 m depth, 9 Apr 1980, R. Sims, s. n. (MICH); SW of Carrie Bow Cay, 3.0 m depth, 25 Mar 1980, M. Hay, s. n. (UC, US), and on coral rubble, patch reef, 6.1–9.1 m depth, 1 Apr 1985, M. Littler, JN-12477 (US), and under coral head, patch reef, 5–8 m depth, 5 Apr 1989, J. Norris, K. Bucher & C. Pueschel, JN-16241 (US); SE of Carrie Bow Cay, patch reef, 4.6 m depth, 28 Apr 1980, R. Sims, s. n. (US); vic. of Wee Wee Cay, patch reef, 1.5–7.6 m depth, 25 Nov 1980, K. Bucher, R. Sims, P. Taylor & M. Littler, JN-10138 (US); Blue Ground Range, on *Acropora palmata,* 0.3–1.5 m depth, 10 Apr 1985, C. Tanner, JN-14830 (US). MARTINIQUE.—between Ilet au Chiens and Pte. Ferre, 8 m depth, 25 Aug 1985, K. Bucher & B. Brooks, KB-1687 (US); Pte. Borgnesse,



Figs. 8–13. Anatomy of *Rhodogorgon carriebowensis.* 8, Transverse section through a third order branch showing cortical cells (c) sharply demarcated from the medullary region (m) of intertwined rhizoidal filaments (unstained, Nomarski). 9, Close-up of Fig. 8 showing junction between cortex and medulla (unstained, Nomarski). 10–11, Assimilatory filaments organized into cortical fascicles (cf) radially interconnected at their base (arrow), and rhizoidal filaments (arrowhead) cut off from innermost cortical cell bearing fascicle (Nomarski). 12, Close-up of base of cortical fascicle, showing pseudotrichotomous branching (arrow), uninucleate cortical cells and

3.0–18.3 m depth, 23 Aug 1985, M. Hay, KB-1264 (US), to 12.2 m depth, 24 Aug 1985, M. Hay & L. Fisher, KB-1645 (US), and 5 m depth, 29 Aug 1985, M. Hay & K. Gustafson, KB-768 (US); Passe du Marin, off Pte. Borgnesse, 3.0–12.2 m depth, 28 Aug 1985, K. Bucher & B. Brooks, KB-1438 (ADU, MELU, UC, US), and 12 m depth, 28 Aug 1985, M. Hay & L. Fisher, KB-1447 (BISH, MICH, US). PANAMA.—Galeta Reef, N of STRI's Galeta Lab., 1 Jul 1978, M. Hay, MH-193 (US); San Blas Islands, SW side of Sail Rock, 6.1 m depth, 8 Aug 1979, J. Norris, s. n. (US).

Rhodogorgon ramosissima
J. Norris et Bucher, sp. nov.
Figs. 6–7

Diagnosis.—Thallus compactus ad 30 cm, obscure canescens vel atrovirens, plusminusve radialiter et profuse ad 5-plo ramosus; ramis distaliter tenuiorious ultimis brevis in diametro uniformibus. Cortex as 105 μm diam.; cellulis medullosis 3–4 μm latis et plerumque 140 μm longis; cylindricis calciferis plusminusve 27 μm longa et 12 μm diam.

The thalli of *R. ramosissima* are usually more compact and densely, more or less radially, branched to five orders, with the branches becoming progressively smaller outwards. The ultimate branchlets are short, of uniform diameter and have blunt apices. The color of *R. ramosissima* is generally darker, dark grey to blackish-green; the medulla and cortex are distinct, with the cortical layer to 105 μm wide; medullary cells 3–4 μm in diam. and mostly 110–150 μm long; the calcite structures of the calciferous cells are 12 μm diam. by 27 μm long.

Remarks.—This species differs from *R. carriebowensis* primarily in habit, being more densely branched, up to five orders. Branching tends to be radial, with the branches becoming progressively smaller and shorter outwards. The ultimate branches are short, apparently determinate, and of uniform diameter with blunt apices. The specific epiphet, *ramosissima,* is derived from *ramosus,* full of branches, and *-issimus* (adjectival superlative) meaning very or most. The air-dried herbarium specimens of *R. ramosissima* are similar to the gorgonian, *Plumigorgia.*

Type.—Carlisle Bay, Antigua, Lesser Antilles, on rocks, 0.5–6.1 m depth, 21 Aug 1985, K. E. Bucher & B. L. Brooks KB-1271a (holotype: Alg. Coll. US-098361; isotype: Alg. Coll. US-098362).

Distribution.—Caribbean Sea: Antigua and Martinique, Lesser Antilles.

Paratypes—Caribbean Sea: ANTIGUA.—Carlisle Bay, 0.5–6.0 m depth on rocks, 21 Aug 1985, K. Bucher & B. Brooks, KB-1271b (ADU, BISH, MELU, MICH); vic. Cade Reef, 10.7 m depth, 21 Aug 1985, K. Bucher, B. Brooks, & W. Fenical, KB-1551 (US). MARTINIQUE—near Petite Martinique in Havre du Robert, 1.5–3.0 m depth on rocks, 25 Aug 1985, W. Fenical, KB-1691 (MICH, UC, US); Pte. Borgnesse, 12.2 m depth, 24 Aug 1985, M. Hay & L. Fisher, KB-1647 (US); Ilet Rainville, 6.1 m depth, 26 Aug 1985, M. Hay, KB-699 (US).

Results.—The absorption spectrum peaks of the red algal phycobilisomes (Gantt 1981) of *R. carriebowensis* are 497 nm and 565 nm, indicating R-phycoerythrin as known only in the red algae. The fluorescence spectrum peak is 578 nm, indicating phycoerythrins as found in both red and blue-green algae. Comparative thin layer chromatographs revealed no apparent unusual secondary metabolites in the lipid extract. This suggests that *Rhodogorgon* is not chemically

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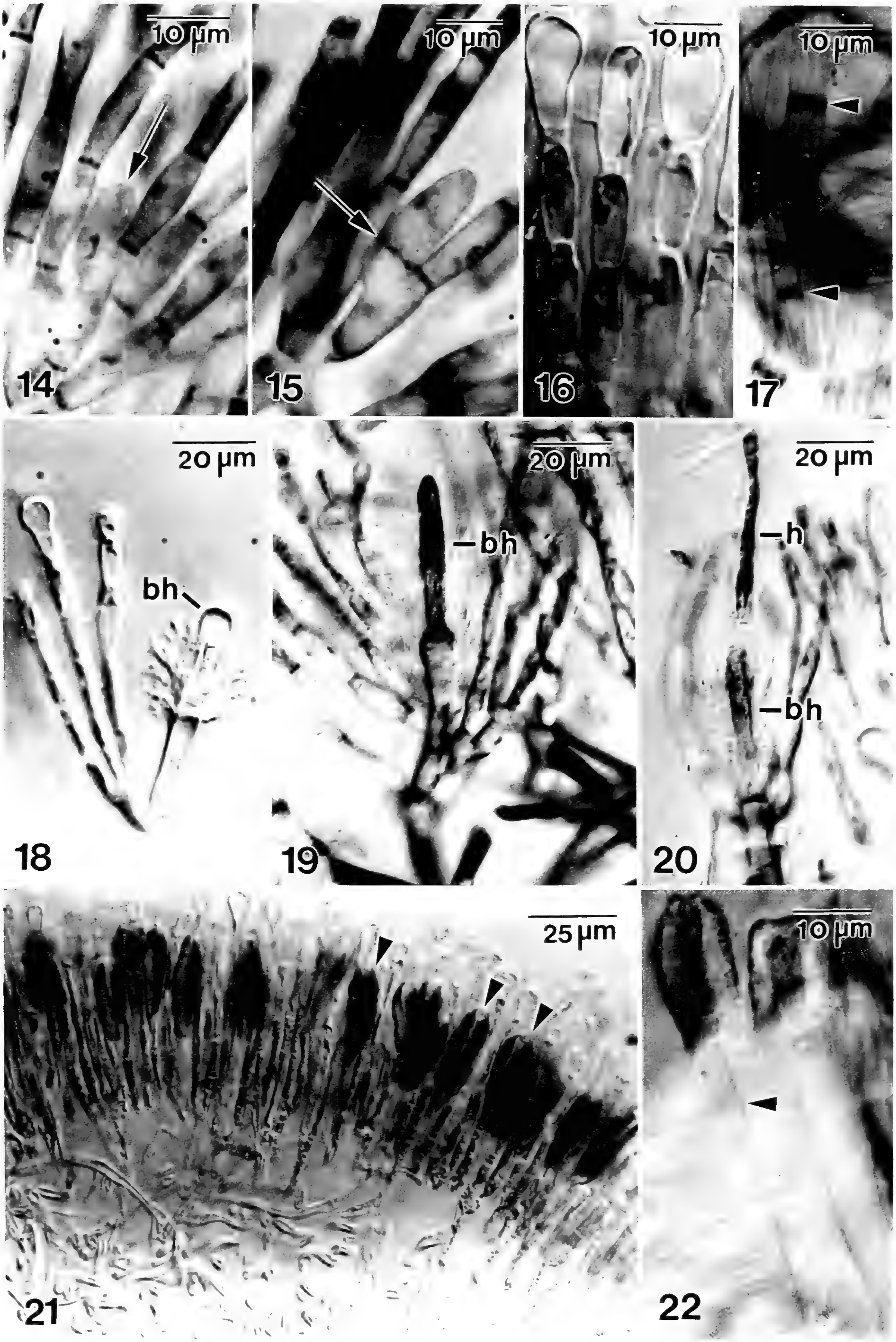
medullary rhizoidal filaments (arrowhead) (hematoxylin stained). 13, Cell within cortical filament budding off part of its cytoplasm distally (arrow) leading to pseudotrichotomy formation, and medullary rhizoidal filaments (arrowhead) cut off from base of cortical fascicle (hematoxylin stained).



Figs. 14–22. Anatomy of *Rhodogorgon carriebowensis.* 14, Cell within cortical filament budding off part of its cytoplasm distally (arrow) leading to pseudotrichotomy formation (hematoxylin stained). 15, Septation (arrow) of protruded cytoplasm leading to new filament is laid down horizontally (hematoxylin stained). 16, Thick-

defended (sensu Norris & Fenical 1982) against herbivory. Because of its resemblance to certain soft corals, we suggest it may elude predation as a gorgonian mimic.

Recently, hydroxy fatty acids chemically related to mammalian prostaglandins and leukotrienes have been isolated from the tropical red alga *Platysiphonia miniata* (Moghaddam et al. 1989). Studies on fresh homogenates of *R. carriebowensis* showed it apparently contains significant lipoxygenase activity resulting in the formation of a product with a UV absorbance spectrum indicative of conjucated diene. *Rhodogorgon* also appeared to contain measurable phospholipase A activity. The presence of these two enzymes suggests that *Rhodogorgon* may be capable of producing biologically active eicosanoid-like compounds (metabolites of arachidonic acid), thus far only known in these red algae.

The life history of *Rhodogorgon* is presently unknown. Because it is infrequently encountered and usually sparse where found, it may have a microscopic, filamentous or other hetermorphoric alternate not yet recognized. No tetrasporophytes of *Rhodogorgon* have been field collected, although they and its life history would likely have systematic implications.

Discussion.—A striking feature of *Rhodogorgon* is the presence of localized calcite deposits that envelop unsegmented, elongate, hair-like cells with inflated tips. These calciferous cells are cut off from the base of cortical fascicles and are not known to occur in any other alga. In the calcareous red algae, calcite is an unusual mineral form of calcium carbonate. The Corallinales (Silva & Johansen 1986) are the only other red algae known to precipitate calcium carbonate in this form; all other known calcified red algae possess aragonite (Borowitzka et al. 1974, Littler 1976). The Corallinales are considered to be an ancient group, having been found in limestone deposits from the late Cretaceous (Littler 1972), and extending as far back as the Jurassic (Johansen 1981). If calcite is the ancestral mode of calcium carbonate precipitation, perhaps *Rhodogorgon* is also a very old taxon.

The function of the calcite structures borne on the calciferous cells of the cortical fascicles is still unknown. Because the calcite is localized and only in the apical region, the cells may be involved in secondary branch formation and contribute to thallus structure. They could also play a role in nutrient boundary layer breakdown, or may be herbivore deterrents.

Ultrastructural features of pit-plugs have been useful in postulating phylogenetic affinites at ordinal levels (Pueschel & Cole 1982, Pueschel 1989). Presence of a dome-shaped outer cap layer on the pit plug is, besides *Rhodogorgon,* only reported in the Corallinales, Batrachospermales and some Acrochaetiales (Pueschel 1989). Since *Rhodogorgon* shares morphological characteristics with the former two orders, it will be briefly compared with them for possible taxonomic affinities. Although *Rhodogorgon* shares pit plug characteristics and calcite with the Corallinales, their vegetative and reproductive morphologies are very different. *Rhodogorgon* is unique among all the algae in the location and specialized structures of calcium carbonate deposits (for

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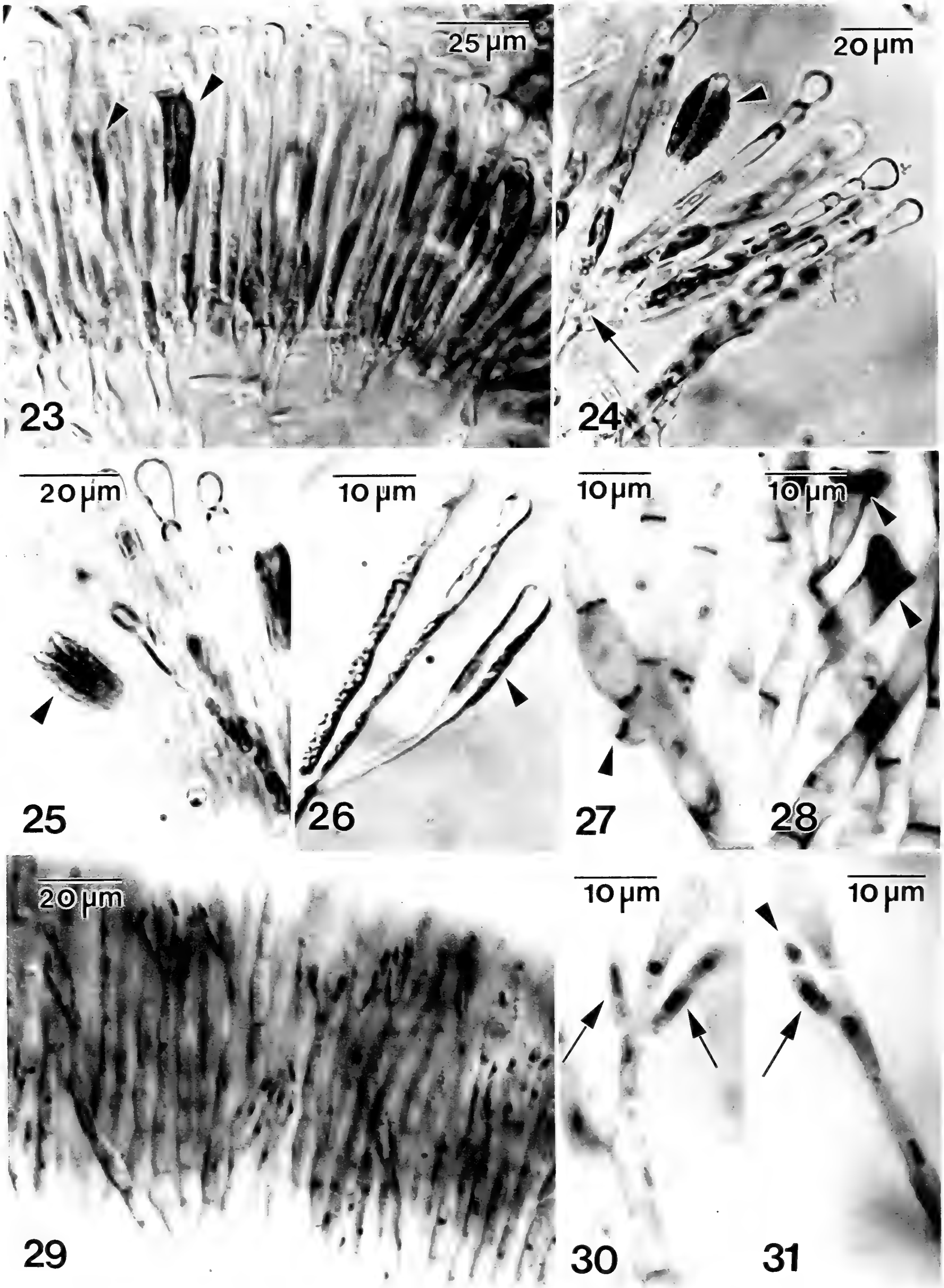
walled, vacuolate, inflated mature terminal cells of assimilatory filaments; chloroplasts of intercalary cortical cells are parietal (unstained, Nomarski). 17, Close-up of thick-walled, medullary rhizoidal filament showing pit-connection and pit ring (arrowhead) (hematoxylin stained). 18, Basal cell (bh) of hair erupting cellulose fibrils from cell wall (unstained, Nomarski). 19, Darkly stained basal cell (bh) that will develop a hair cell (hematoxylin stained, Nomarski). 20, Densely staining hair cell (h) pit-connected to its basal cell (bh) (hematoxylin stained, Nomarski). 21, Calcite surrounded apices (arrowheads) of elongate, calciferous cells embedded in cortex (unstained, Nomarski). 22, Narrow channel within wall of a calciferous cell (unstained).



Figs. 23–31. Anatomy of *Rhodogorgon carriebowensis*. 23, Hyaline, elongate, calciferous cells with calcite structures (arrowhead) located among the cortical filaments (unstained, Nomarski). 24, Elongate calciferous cell, bearing calcite structure (arrowhead), that is pit-connected (arrow) to base of pseudotrichotomy (unstained). 25, Formation of a longitudinal furrow within calcite covered apex (arrowhead), and emergence of inflated tip of a calciferous cell (unstained). 26, Calciferous cell at base of a pseudodichotomy, and partially dissolved calcite deposit (arrowhead) (unstained, Nomarski). 27, Pseudotrichotomy with basally pit-connected (arrowhead) remnant of a calciferous cell (hematoxylin stained). 28, Apical portion of a calciferous cell which is separated from

summary of calcification in the algae, see Littler & Littler 1984). The domoid expansion of the outer cap layer on the pit plug may be a primitive trait. If possession of a dome-shaped outer cap is ancestral, it may again indicate that *Rhodogorgon* is a very old taxon.

Among the Batrachospermales, *Rhodogorgon* is morphologically most similar to *Thorea* in the Thoreaceae, a family recently transferred from the Nemaliales to the Batrachospermales (Pueschel & Cole 1982). In contrast to the Thoreaceae, other members of the Batrachospermales are uniaxial and composed of axial filaments of indeterminate growth surrounded by whorled lateral filaments of limited growth (Aghajanian & Hommersand 1980). The Thoreaceae are multiaxial (Swale 1962, 1963; Yoshizaki 1986). In both *Rhodogorgon* and *Thorea* the basal cells of assimilatory branches produce rhizoidal filaments that contribute to the structure of the medulla. However, their cortical fascicles differ, being basically pseudotrichotomous in *Rhodogorgon* and pseudodichotomous in *Thorea.* Also, *Rhodogorgon* is marine and calcified, whereas the Thoreaceae are exclusively freshwater (Sheath 1984) and lack calcification. Interestingly, two different types of carposporophyte development have been described for two species currently placed in *Thorea.* In *T. bachmannii* Pujals ex Pujals from Brazil, Necchi (1987) illustrated a compact carposporophyte, whereas Yoshizaki (1986) observed a diffuse carposporophyte in *T. okadai* Yamada from Japan. These differences could indicate that the Thoreaceae may be polyphyletic, and that some members of the family (e.g., *T. okadai*) may be more closely related to some of the Nemaliales, such as *Dotyophycus* (Abbott & Yoshizaki 1981) and *Yamadaella* (Abbott 1970), and others, such as *T. bachmannii,* to the Batrachospermales. So far, only *T. riekei* Bischoff (1965) has been investigated for pit plug morphology, and if *T. okadai* lacks an outer dome pit plug cap, it would be more related to the Nemaliales. The systematic position of *Thorea* needs to be critically reinvestigated.

Rhodogorgon shares certain anatomical similarities with some members of the Galaxauraceae Parkinson and Liagoraceae Kützing of the Nemaliales. Although both families contain some calcareous members, they possess only aragonite (Borowitzka et al. 1974, Littler 1976, Okazaki et al. 1982). Apical depressions containing an apical cell that directs cell growth in members of Galaxauraceae were not seen in *Rhodogorgon,* but the presence of intertwined medullary filaments is reminiscent of *Galaxaura* and *Scinaia.* In the latter genera, basal cells of the cortical filaments cut off rhizoids and the process of cortex differentiation is mainly one of vacuolization accompanied by inflation in the terminal utricles (see Ramus 1969, for *Scinaia,* as '*Pseudogloiophloea*'). One could envision that appression of the utricles in the Galaxauraceae is a more advanced trait than the non-appressed terminal inflations of *Rhodogorgon.* There are also reproductive differences. The male reproductive structures are very simple in *Rhodogorgon,* while in some Galaxauraceae (i.e., *Galaxaura, Actinotrichia, Nothogenia*) the spermatangial parent cells are organized within specialized conceptacles (Svedelius 1939, 1943; Magruder 1984); the other gen-

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←

the remaining portion by a lenticular wall (arrowhead), observed after dissolution of the calcite (hematoxylin stained). 29, Cortex with spermatangial parent cells and spermatangia (hematoxylin stained, Nomarski). 30, Pair of spermatangial parent cells (arrows) borne bilaterally on subterminal cell of cortical filament (hematoxylin stained). 31, Spermatangium (arrowhead) cut off singly from a spermatangial parent cell (arrow) (hematoxylin stained).

era produce spermatangia at the thallus surface (e.g., Huisman 1986 for *Scinaia*). The spermatangial configuration of *Rhodogorgon* is certainly simpler than in the calcified members of the Galaxauraceae.

In the Nemaliaceae (Farlow) DeToni et Levi and the Liagoraceae, main axes and branches are of the multiaxial 'Springbrunnen-type' (Oltmanns 1922), and thus very different from the vegetative anatomy of *Rhodogorgon* which lacks a central core of axial medullary filaments. The origin of spermatangial parent cells in *Rhodogorgon* is nevertheless reminiscent of that of *Yamadaella* (Liagoraceae), where spermatangial parent cells are borne on subterminal cells of cortical filaments (Abbott 1970). Spermatangial parent cells in *Yamadaella* frequently cut off a short chain of spermatangia (Abbott 1970), whereas those of *Rhodogorgon* were only seen to cut off a single spermatangium. *Yamadaella* and *Rhodogorgon* both have inflated terminal cells on their assimilatory filaments.

Conclusions.—Based on vegetative and reproductive anatomy, our light-microscope studies suggest that *Rhodogorgon* exhibits similarities with some Thoreaceae, Galaxauraceae and Liagoraceae, whereas based on pit plug morphology, it shows relationships with *Thorea* and *Nemalionopsis* of the Thoreaceae (Pueschel & Cole 1982, Pueschel 1989). However, it differs in several characteristics from all of these families, and based on its combination of unusual characters, we are of the opinion that the new genus is only ancestrally related to the families mentioned above, or via convergence has evolved some similiar characteristics. *Rhodogorgon* is hypothesized to be a primitive red alga that may have originated before the families of the Nemaliales were present and diversified, and so we believe it would be better placed in a family of its own. However, this assessment must await more detailed studies on the development of the female reproductive system, life history, and ultrastructural characteristics.

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THE HIGH FREQUENCY OF ERRORS IN FORMAT IN MANUSCRIPTS SUBMITTED TO *PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON*

Thomas E. Bowman

Abstract.—Failures to conform to 25 items of *Proceedings* style are enumerated for 40 manuscripts submitted for publication. Up to 15 errors/manuscript were found, with a mean of 4.85 errors/manuscript. Authors are urged to improve this record.

Having recently reached the 7th decade of my life and having served as Associate Editor for Invertebrates for 14 years, I have decided to give up that position and spend more time on research projects to which I am committed. Hoping to make my successor's task easier, I wish to call attention to the high frequency of failures by authors to conform to the format of the *Proceedings.* Such failures increase unnecessarily the burdens of the editors and in most cases could easily be avoided.

I chose 25 items of format and analyzed 40 randomly selected manuscripts for conformity with these items. The items are listed below, arranged in 10 categories. Following each format item is the number, and in parentheses, the percentage of manuscripts containing that error of format.

I. Address(es) of author(s)
    1. Address(es) omitted—2 (5%)
    2. Address(es) in wrong place—13 (32.5%)
II. Abstract
    3. Abstract missing—2 (5%)
    4. "Abstract" a center instead of a side heading—12 (30%)
III. Center headings (e.g., name of a family, Acknowledgments, Literature Cited)
    5. Side heading used instead of center heading—4 (10%)
    6. Center heading in italics—2 (5%)
    7. Center heading in all capitals—17 (42.5%)
IV. Side headings
    8. Side heading not indented—16 (40%)
    9. Side heading in wrong format (e.g., in all capitals, all words capitalized, colon used instead of period and dash)—13 (32.5%)
V. Synonymies
    10. Punctuation incorrect—3 (7.5%)
    11. Names of journals included–2 (5%)
VI. Citations of references in text
    12. Punctuation incorrect, e.g., "Smith, 1960, p. 10" instead of "Smith 1960:10"—6 (15%)
VII. References in text to figures
    13. "Figure" instead of "Fig."—5 (12.5%)
    14. "fig." instead of "Fig."—5 (12.5%)
VIII. Citations of dates in *Materials* sections
    15. Failure to use day-month-year and 3-letter abbreviation without period for month, e.g., 15 Jun 1960—7 (17.5%)
IX. Literature Cited
    16. Literature Cited single spaced—3 (7.5%)
    17. Names of journals abbreviated—11 (27.5%)
    18. Names of journals in italics—3 (7.5%)
    19. Words in titles of articles capitalized—3 (7.5%)

    20. Punctuation of authors' names incorrect—14 (35%)
    21. Pagination lacking or incomplete—2 (5%)
    22. Indentation incorrect—4 (10%)
X. Legends for illustrations
    23. "Figure" used instead of "Fig."—10 (25%)
    24. Indentation incorrect—19 (47.5%)
    25. Punctuation incorrect—17 (42.5%)

A total of 194 of the 25 kinds of format errors was found in the 40 manuscripts. The number of errors/manuscript ranged from 0–15, with a mean of 4.85 and a mode of 4. Thus the average manuscript contained errors in about ⅛ of the format items. Only ⅒ of the manuscripts were free of format errors.

Of the 25 format items, directions are given for 8 in "Information for Contributors" on the inside back cover of each issue of the *Proceedings*. The other 17 should be apparent to any author who examines a recent issue. *Proceedings* editors are uncompensated volunteers. Please be kind to them by doing your best to follow *Proceedings* format; it does not require great effort or sacrifice to do so, and it will speed up the editorial processing of your manuscript.

Department of Invertebrate Zoology, National Museum of Natural History NHB-163, Smithsonian Institution, Washington, D.C. 20560.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Call for nominations for New Members of the International Commission on Zoological Nomenclature

The following members of the Commission reach the end of their terms of service at the close of the XXIV General Assembly of the International Union of Biological Sciences to be held in Amsterdam, in July 1991: Dr. H. G. Cogger (Australia, Herpetology); Prof Dr O. Kraus (Fed. Rep. Germany, Arachnology); Dr M. Mroczkowski (Poland, Coleoptera); Dr W. D. L. Ride (Australia, Mammalia). A further vacancy arises from the resignation of Dr G. C. Gruchy (Canada, Ichthyology).

The addresses and specialist fields of the present members of the Commission may be found in the *Bulletin of Zoological Nomenclature,* 46(1) (March 1989). Under Article 3*b* of the Commission's Constitution a member whose term of service has terminated is not eligible for immediate re-election unless the Council of the Commission has decided to the contrary.

The Commission now invites nominations, by any person or institution, of candidates for membership. Article 2*b* of the Constitution prescribes that:

"The members of the Commission shall be eminent scientists, irrespective of nationality, with a distinguished record in any branch of zoology, who are known to have an interest in zoological nomenclature."

(It should be noted that "zoology" here includes the applied biological sciences (medicine, agriculture, etc.) which use zoological names).

Nominations made since September 1987 will be reconsidered automatically and need not be repeated. Additional nominations, giving the date of birth, nationality and qualifications (by the criteria mentioned above) of each candidate should be sent by 15 June 1990 to: *The Executive Secretary, International Commission on Zoological Nomenclature, % British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.*

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications Published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 23 June 1989 in Vol. 46, Part 2 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

Case No.

2657 *Marssonopora* Lang, 1914 (Bryozoa, Cheilostomata): proposed designation of *Membranipora densispina* Levinsen, 1925 as the type species.
2403 *Valanginites* Sayn in Kilian, 1910 (Cephalopoda, Ammonoidea): confirmation of the author of the genus, and of *Ammonites nucleus* Roemer, 1841 as its type species.
2642 POLYGYRIDAE Pilsbry, 1894 (Mollusca, Gastropoda): proposed precedence over MESODONTIDAE Tryon, 1866.
2666 *Lucicutia* Giesbrecht in Giesbrecht & Schmeil, 1898: proposed conservation, and *Pseudaugaptilus longiremis* Sars, 1907: proposed conservation of the specific name (both Crustacea, Copepoda).
2624 *Ranguna* Bott, 1966 and *Larnaudia* Bott, 1966 (Crustacea, Decapoda): proposed fixation of *Thelphusa longipes* A. Milne Edwards, 1869 and *Thelphusa larnaudii* A. Milne Edwards, 1869 as the respective type species.
2542/2 *Trapezia* Latreille, 1828 (Crustacea, Decapoda): proposed conservation.
2656 *Chira* Simon, 1902 (Arachnida, Araneae): proposed conservation.
2647 *Heliophanus kochi* Simon, 1868 (Arachnida, Araneae): proposed conservation of the specific name.
2648 *Attus penicillatus* Simon, 1875 (currently *Sitticus penicillatus*; Arachnida, Araneae): proposed conservation of the specific name.
2649 *Thyene* Simon, 1885 (Arachnida, Araneae): proposed conservation.
2677 *Saissetia* Déplanche, 1859 (Insecta, Homoptera): proposed designation of *Lecanium coffeae* Walker, 1852 as the type species.
2695 *Fonscolombia* Lichtenstein, 1877 (Insecta, Homoptera): proposed designation of *Fonscolombia graminis* Lichtenstein, 1877 as the type species.
2665 *Rosema* Walker, 1855 (Insecta, Lepidoptera): proposed conservation.
2658 *Protocalliphora* Hough, 1899 (Insecta, Diptera) and its type species *Musca azurea* Fallén, 1817: proposed conservation of usage by designation of a replacement lectotype.
2659 *Osteoglossum* Cuvier, 1829 (Osteichthyes, Osteoglossiformes): proposed fixation of *O. bicirrhosum* (Cuvier, 1829 as the name of the type species.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Opinions published in the *Bulletin of Zoological Nomenclature*

Opinion No.

1536 *Sorites* Ehrenberg, [1839] (Foraminiferida): *Nautilus orbiculus* Forsskål, 1775 designated as the type species.

1537 *Discocyclina* Gümbel, 1870 (Foraminiferida): *Orbitolites prattii* Michelin, 1847 designated as the type species.

1538 *Disculiceps* Joyeux & Baer, 1935 (Cestoidea): conserved.

1539 *Conus floridanus* Gabb, 1869 (Mollusca, Gastropoda): not to be given precedence over *Conus anabathrum* Crosse, 1865.

1540 *Avicula gryphaeoides* J. de C. Sowerby, 1836 (Mollusca, Bivalvia): specific name conserved.

1541 *Loxoconchella* Triebel, 1954 (Crustacea, Ostracoda): *Loxoconcha honoluliensis* Brady, 1880 confirmed as the type species.

1542 *Chelifer* Geoffroy, 1762 (Arachnida, Pseudoscorpionida): conserved.

1543 *Dytiscus cinereus* Linnaeus, 1758 (currently *Graphoderus cinereus*; Insecta, Coleoptera): neotype replaced.

1544 ETHMIIDAE Busck, 1909 (Insecta, Lepidoptera): given precedence over AZINIDAE Walsingham, 1906.

1545 *Glabellula* Bezzi, 1902 (Insecta, Diptera): *Platygaster arcticus* Zetterstedt, 1838 designated as the type species.

1546 *Chelonus* Panzer, 1806 (Insecta, Hymenoptera) and *Anomala* Samouelle, 1819 (Insecta, Coleoptera): names conserved.

1547 *Silurus felis* Linnaeus, 1766 (currently *Ariopsis felis*; Osteichthyes, Siluriformes): neotype designated.

1548 *Sarotherodon melanotheron* Rüppell, 1852 (Osteichthyes, Perciformes): specific name conserved.

BIOLOGICAL SOCIETY OF WASHINGTON

116th Annual Meeting, 25 May 1989

The meeting was called to order by Kristian Fauchald, President, at 12:00 noon in the Waldo Schmitt Room, National Museum of Natural History.

Don Wilson, Treasurer, reported that income from dues in 1988 was about equal to that of 1987, and that income from subscriptions, sales of past issues of the Proceedings, and page charges was substantially higher than in 1987, the latter showing an increase of about $10,000. Total income for 1988 was $100,185 and total expenditures were $87,224. The proposed budget for 1989 balances an estimated income of $94,000 with equal estimated expenditures. The Treasurer's Report was unanimously accepted.

Brian Robbins, Editor, then reported on Volume 101 of the Proceedings. Ninety-nine papers, totaling 977 pages, were published in 1988. Brian noted that unpaid papers currently make up about 300 pages of the Proceedings per year and are subject to a publication delay of approximately one year. Papers with full funding generally have less than a year (about three issues) delay. All manuscripts with full funds submitted in 1988 and some from 1989 will be published in 1989. Brian announced several changes in Associate Editors during the past year. For Vertebrate Zoology, G. David Johnson replaced Richard P. Vari; for Invertebrate Zoology, Frank D. Ferrari and Raymond B. Manning replaced Thomas E. Bowman; for Entomology, Wayne N. Mathis replaced Robert D. Gordon. Brian noted that substantial progress has been made on the One-Hundred Year Index. Once family coding for each paper has been completed, Phyllis Spangler will produce camera-ready copy for publication as a special issue of the Proceedings, to appear sometime in 1990. The Editor's Report was accepted without comment.

Kristian announced that we will need a new Custodian of Publications to replace Dave Pawson who will be stepping down at the end of May (Austin B. Williams has accepted those duties).

A motion was made and seconded that the meeting be adjourned; Kristian adjourned the meeting at 12:25 p.m.

Respectfully submitted,
G. David Johnson
Secretary

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with a summary in an alternate language when appropriate.

Submission of manuscripts.—Submit manuscripts to the Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed in order of receipt by a board of Associate Editors and appropriate referees.

Proofs.—First proofs are submitted to authors for correction and approval. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, changes at proof stages, and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

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The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's(s') Address(es), Appendix, Figure Legends, Figures (each numbered and identified), Tables (**double-spaced throughout,** each table numbered with an Arabic numeral and with heading provided).

Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is required for descriptions and diagnoses. Literature citations in the text should be in abbreviated style (author, date, page), except in botanical synonymies, with unabbreviated citations of journals and books in the Literature Cited sections. Direct quotations in the text must be accompanied by author, date, **and pagination.** The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Examples of journal and book citations:

Eigenmann, C. H. 1915. The Cheirodontidae, a subfamily of minute characid fishes of South America.—Memoirs of the Carnegie Museum 7(1):1–99.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate figure and table placement in pencil in the margin of the manuscript. Plan illustrations in proportions that will efficiently use space on the type bed of the Proceedings. **Original illustrations should not exceed 15 × 24 inches.** Figures requiring solid black backgrounds should be indicated as such when the manuscript is submitted, but should not be masked.

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